Inference of foraging success in a top Southern Ocean predator

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2 Statement of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person except where due acknowledgment is made in the text of the thesis

19/09/2019

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Abstract

Acquiring resources is the foremost activity that any organism must succeed at, given all other aspects of an animal's life-history (growth, survival and reproduction) depend upon how successful an individual is at foraging. Despite the central importance of foraging, quantifying foraging success remains difficult in the wild and especially so in the marine environment. Here, direct observations or real-time measurements are particularly challenging. It is often not possible to get *in-situ* information, especially from highly migratory species - like seals - that spend many months in remote oceanic realms. Most of the knowledge about at-sea feeding behaviour is generated by instrumenting free-living organisms and drawing inference from their tracking and/or diving data. Many different types of behaviours, including those associated with foraging events, can be inferred but the actual foraging success remains elusive.

This study is concerned with the quantification of foraging success for southern elephant seals (*Mirounga leonina*), a large marine predator widely distributed in the Southern Ocean. Elephant seals are an ideal study organism because they spend most of their lives at sea feeding but return to their natal sub Antarctic islands to breed and moult, enabling tagging and in some cases recovery of electronic instruments that record their at-sea behaviours. Importantly, southern elephant seals are one of the few species known to perform a special dive type, called drift dives, which allow changes in body condition to be quantified. Drift dives are characterized by a long, inactive phase; during this phase, the rate of change in depth is determined by the buoyancy of the seal, ultimately linked to the ratio of lean:fat tissues. If these drifting segments are correctly identified, then the *in-situ* body condition and its changes through time become tractable. However, since in many cases dive information is actually transmitted through satellite systems, this data must be summarized by on-board algorithms before transmission. This loss of resolution hampers identification of drift dives; furthermore, changes in summarization algorithms have limited the development and widespread use of drift rate as a measure of body condition from summarized dive datasets that are now commonly available for this species.

In this thesis, I present my original research on:

(1) *Drift dive identification and drift rate estimation.* By developing a flexible, hierarchical approach for detecting drift dives and estimating the body condition of southern elephant seals from summarized dive profiles, I overcome a long-term challenge due to changes in dive

summarization algorithms. Validation with independent datasets shows the method retains approximately 3% of all dives, of which 88% are true drift dives, and the drift rate estimates are unbiased. The trend of the drifting time-series match expectations for capital breeders, showing the lowest body condition commencing foraging trips and a progressive improvement as they remain at sea. This method to is now publicly available to the research community in the form of an open source R package, enabling at-sea changes in condition to be robustly estimated for large existing and ongoing data collections with potential for application across other drift diving species.

(2) *The importance of the polynyas as a foraging habitat for Antarctic predators.* Southern elephant seals forage in a diverse range of ocean habitats and recent research has highlighted their usage of Antarctic coastal polynyas (recurrent areas of open water in the sea-ice). By implementing the method developed in part 1 above, I develop body condition indices and provide for the first time quantitative evidence of enhanced foraging success for those southern elephant seals (primarily males) targeting the polynya areas, in comparison to those animals using the rest of the shelf and surrounding Antarctic waters. My results confirm the relative importance of polynyas as specific areas of the Antarctic region that are regularly targeted by seals and other air-breathing marine predators

(3) *Predicting drift dive changes in relation to diving behaviour*. I investigate the correspondence between drift-rate indices and a suite of dive metrics traditionally related to the body condition and buoyancy. I have found similar results to those obtained via high resolution time-depth recorders and accelerometer data, but using an extensive data-base of tracked elephant seals from the Indian sector of the Southern Ocean of compressed dive information. The relationships found between the body condition and different dive metrics expand previous research by improving the ability to infer the body condition from simple dive metrics. The results also demonstrate the apparent benefits of seals being near neutral buoyancy, as predicted by the literature. Considering elephant seals as ‘surfacers’ (i.e., well adapted air-breathing organisms that in fact spend most of their time at sea, deep diving and returning only briefly to the surface to breathe), I argue they should be expected to maximize their diving efficiency, irrespective of whether they are foraging or not. However, , elephant seals are found increase their diving efficiency under favourable foraging scenarios.

Statement of co-authorship

Statement of Co-Authorship

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

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Wrote the manuscript: F. Arce with contributions from all the co-authors

R package: Located in Chapter 3

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We, the undersigned, endorse the above stated contribution of work undertaken for each of the published (or submitted) peer-reviewed manuscripts contributing to this thesis:

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Chapter 1

1.1 Introduction

All living organisms must acquire enough resources to fulfil their energetic demands (Stearns 1992). In order to survive and succeed organisms must become effective foragers while avoiding predation (Verdolin 2006, Higginson and Houston 2015), as almost all species are susceptible to being predated by others. How successful an individual is at foraging, and how much energy is acquired (relative to its own energetic demands), will determine how much energy will be available to allocate into reproduction without compromising future survival (Stearns 1992, Audzijonyte and Richards 2018). How long an animal is able to avoid a fatal encounter with predators, pathogens or accidents will determine the length of its life as a breeder, and the number of offspring produced (Lind and Cresswell 2005, Sansom et al. 2009). These basic individual-based requirements translate to population trajectories as they govern who lives and dies, who breeds or doesn't, and ultimately, how much a given individual will contribute to future generations (Brommer et al. 2002, Reid et al. 2019). The better an organism is at foraging, and the better it is at keeping itself alive, the greater its contribution to the gene pool of the population and ultimately the maintenance of its own genes in future generations. These predation relationships between species further govern energy fluxes trough trophic levels, from primary producers to apex predators, and are the basis of ecosystem function and stability (Barnes et al. 2018, Gounand et al. 2018). This study considers the foraging success of a large Southern Ocean marine predator, the southern elephant seal (*Mirounga leonina*).

Search strategies play an important role in foraging success. Prey fields are not homogeneously distributed in space and time, especially in marine systems (Fauchald 1999), so a simple, random search strategy may not be the optimal way to maximize prey encounters and energy intake (Sims et al. 2008). Depending on the specific life-histories of different species, the optimal strategies can vary considerably (a few very notable examples might include highly migratory species, capital vs income breeders, deep sprint divers and bulk feeders etc.). Some species may have more than one foraging strategy, either due to individual and environmental heterogeneity, or due to seasonal variations in individual requirements and/or prey availability (Breed et al. 2009, Rayl et al. 2018, Gilmour et al. 2018). Many species are attached to their nest or territories

during the breeding season and need to forage in a way that allows them to return frequently to provision their offspring, known as a *central place foraging* strategy (Orians and Pearson 1979, Houston and McNamara 1985). Other species, like elephant seals, are capital breeders that fast during the breeding season and rely on the energy acquired beforehand to sustain them and their young during breeding (Fedak et al. 1996, Fowler et al. 2018). After the breeding season, some species will remain foraging near the breeding grounds, while others will migrate, exhibiting short to long distance movements (wildebeest (*Connochaetes gnou*), albatross (family Diomedeidae)), or even well-defined trans-hemispheric seasonal movements like sooty (*Ardenna grisea*) (Shaffer et al. 2006) and short-tailed shearwaters (*Ardenna tenuirostris*) (Carey et al. 2014) and humpback whales (*Megaptera novaeangliae*) (Rasmussen et al. 2007).

Our ability to study a species' foraging ecology depends on the species of interest. Some few species with limited home ranges or conspicuous behaviours can be studied using direct observations, but in many cases direct observations of foraging are hard to obtain. Alternatively, foraging can be inferred; this is often achieved by attaching electronic instruments which measure some aspects of an individual's behaviour in the wild (Rutz and Hays 2009, Wilmers et al. 2015). Arguably, the most widely used animal-borne tags are those which provide information on animal movement – through geographic positioning – either directly (via GPS) or indirectly (e.g. light loggers – geolocators, or by Doppler effect – ARGOS tags).

Animals which live in heterogeneous environments often show periods of direct, fast movements between foraging patches and/or locations; known as *transit behaviour* (Fauchald and Tveraa 2003). While on a foraging patch, movements tend to slow down, and the direction becomes highly variable; known as *area-restricted search* (but see Carter, Bennett, Embling, Hosegood, & Russell (2016) for a critical review on marine organism). These observations matches the theoretical developments around the concept of *optimal foraging theory* (MacArthur and Pianka 1966, Charnov 1976). For some terrestrial species, the areas where the animals appear to be foraging can be inspected directly to gather detailed information on environmental conditions and/or prey abundance.

Most of the areas targeted by marine predators, within the context of the vast and remote Southern Ocean, are seldom explored by oceanographic vessels. Some information relevant for assessing prey fields is available from satellite analysis (e.g. primary productivity) in the form of

proxy indexes of primary productivity (Constable et al. 2003), but this information has some inherent limitations (i.e. they don't obtain information about areas near to or covered by ice, and the information is predominantly limited to the near surface). Physical proxies are therefore commonly used in the absence of direct prey-field information, and in recent years much of the subsurface oceanographic information has actually been generated by seals instrumented with CTD tags that measure conductivity (salinity), temperature, and depth (pressure), among other biophysical variables (Charrassin et al. 2008, Roquet et al. 2014, Treasure et al. 2017). This information is relevant both to understand the physical properties of Antarctic waters, and to allow researchers to link animal behaviour with their immediate physical environment (Malpress et al. 2017, Labrousse et al. 2018).

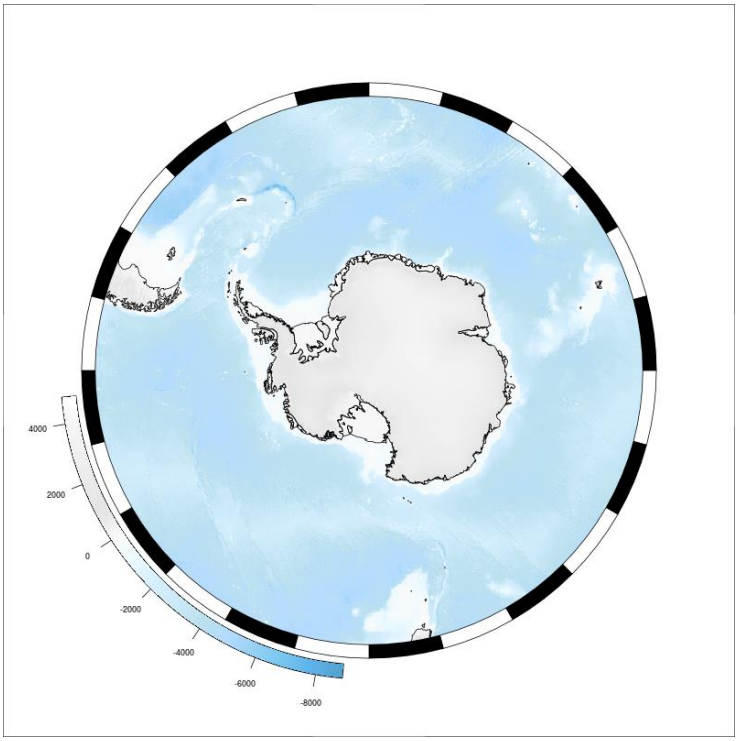

***Figure** 1**.1. Southern Ocean map**. Bathymetry is represented in blue scale (darker being deeper)*

Air-breathing marine predators, such as penguins, seals, or whales typically dive to forage, adding a new (vertical) dimension to the study of their foraging behaviour. Diving presents a major constraint as the animal needs to return to the surface to breathe; this imposes a physiological limit on the diving behaviour and duration that is independent of foraging (Boyd 1997, Kooyman and Ponganis 1998). Diving predators can be split into two main groups: those that spend a large amount of time in the surface, diving to forage (*divers*), and those that spend most of their time at depth, making short visits to the surface to re-oxygenate (*surfacers*) (Kooyman 1989). *Divers* are expected to optimize their dives in terms of oxygen consumption but see Okuyama et al. (2014) as an example of switching behaviours in *surfacers*. They may give up and return early to the surface if they don't locate prey before a certain time threshold has been reached (Thompson and Fedak 2001). However, they may also extend their dives in a good foraging patch (Foo et al. 2016), increasing the number of prey items captured per dive, at the expense of longer post-dive surface periods to recover and reoxygenate (Houston 2011). But the opposite behaviour can be found in 'single item' foragers, which often manipulate prey before being ingested (Houston and McNamara 1985) or if foraging in a good path increases the amount of energy expended per unit of time (Foo et al. 2016). In these circumstances, foraging in a high-density prey field would mean shorter dives, since it would take less time to succeed at catching a single prey item. In comparison, *surfacers* spend most (>80%) of their time diving, returning only briefly to the surface to breathe. As their diving behaviour is not limited only to foraging activities, some of the responses expected from *divers* would not necessarily make sense for *surfacers*. Notably, potential dive abandonment – if no prey is found before a certain threshold – are likely to be less relevant, and should not be expected1.2 Study model: the southern elephant seal

Southern elephant seals have a circumpolar distribution in the Southern hemisphere (Hindell et al., 2016). They breed and moult on Sub Antarctic islands, spending the rest of their time (~80%) at sea, often in extremely remote areas (Figs. 1.1 for the broad distribution range of the southern elephant seal, and 1.2, for the specific region and seal tracks considered in this study). Elephant seals have a dramatic sexual dimorphism, due their polygynous mating system (Fabiani et al. 2004). During the breeding season, males fight for control of beaches and the females under their area of influence, repelling other males from approaching the females congregated within their harem. The females, once having reached sexual maturity (3-6 years old), will try to maximize their fitness by having a long life, adjusting their breeding effort to their own capacity and the environmental conditions (Desprez et al. 2018). For males, breeding status is heavily size dependent and relatively transient. Normally, if they attain beach-master status (only 3-4 % of males are successful), they will be able to maintain that position for only a couple of years .

Thus, maximizing their fitness, and their genetic contribution to future generations, implies concentrating their effort in one or two breeding seasons.

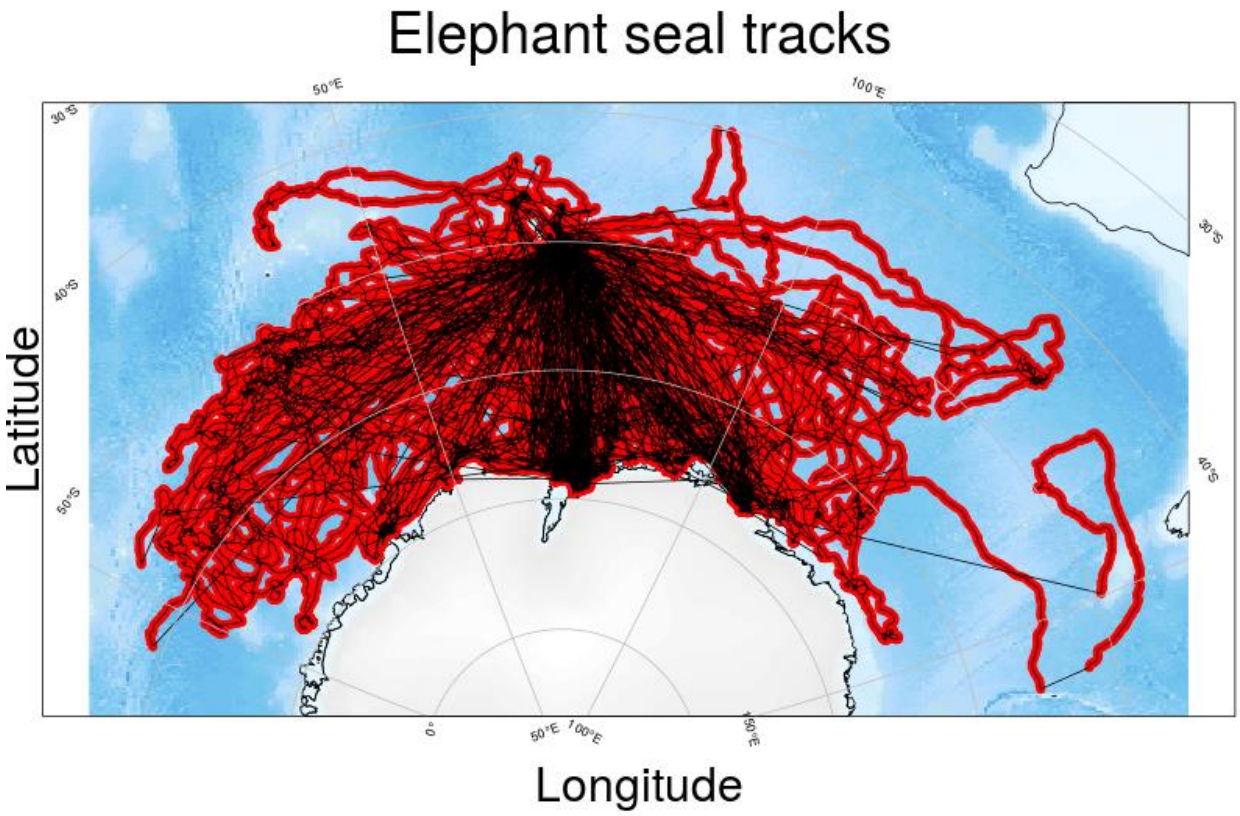

Figure 1.2. Southern elephant seal tracks considered in this study. Red dots represent actual transmitted locations, joined by black lines (N = 231 seals)).

As capital breeders and catastrophic moulters, elephant seals fast during two short periods they spend ashore each year, relying on energetic reserves that must be acquired beforehand during their foraging trips at sea (Stephens et al. 2009). When at sea, elephant seals show broad scale circumpolar distribution along the Southern ocean, from shallower waters close to the colonies to deeper regions of the Southern Ocean or the Antarctic shelf (Hindell et al. 2016), reflecting differences between sexes but also between breeding populations (Jonker and Bester 1998, Field et al. 2001, Bradshaw et al. 2004, Lewis et al. 2006, Muelbert et al. 2013, Labrousse et al. 2015, 2018, Hindell et al. 2016, Malpress et al. 2017). They spend up to 10 months at sea often without visiting any land. Whenseals haul-out, it occurs in remote regions such as small, isolated sub

Antarctic islands (Hindell and Burton 1988, Van Den Hoff 2001) or along the Antarctic coast (Van Den Hoff et al. 2003). Because seals are highly philopatric (they return to breed to the place where they were born) there is virtually no interaction between seals from different populations. As a consequence, four genetically distinct elephant seal breeding populations are recognized, Peninsula Valdes (increasing trend), South Atlantic (stable trend), South Indian (stable trend) and South Pacific (decreasing trend). Two of these – the Southern Indian and the Southern Pacific stocks – breed and forage in Australian Antarctic and Sub Antarctic territories. The Southern Pacific population has shown a steady decline over the last few decades (McMahon et al. 2003), while the Southern Indian stock has become stable after declining through the 1960s and 1980s (McMahon et al. 2005a).

While at sea, elephant seals are best described as *surfacers* (Kooyman 1989). This is because they continuously perform long (> 20 min), deep (> 400 m) dives followed by short surface intervals of between 1-2 minutes (Le Boeuf et al. 1988, Hindell et al. 1991b). Due the small amount of time they spend at the surface, their at-sea distribution and behaviour can only be monitored using animal-borne tags. Commonly these are CTD-SRDLs (Satellite-Relayed Data Loggers that record and transmit vertical profiles of conductivity, temperature and pressure). Because this information must be relayed via the ARGOS satellite system with a limited bandwidth, it needs to be summarized before being transmitted (Fedak et al. 2001, 2002, Photopoulou et al. 2015a). Elephant seals have been the subject of many studies quantifying their diving behaviour (Hindell and Slip 1991, Campagna et al. 1995, 1999, Thompson and Fedak 2001, Lewis et al. 2006, Thums et al. 2013, 2008b, Bailleul et al. 2008, Biuw et al. 2010, McIntyre et al. 2011b, McGovern et al. 2019). Based on the visual appearance of the dive profiles generated by time-depth recorders instrumented on elephant seals, broadly 5-6 types of different dive profiles have been identified (Hindell et al. 1991a), believed to be associated with different behaviours (through the actual behaviour is often uncertain). These profiles are readily detected using high resolution time-depth recorders; however, the compression of information typical from SRDL-CTDs precludes easily identifying dive types and extracting the relevant metrics to reliably assign them to specific animal behaviours.

There is however one specific type of dive, the so-called *drift dive*, that is of particular interest from the point of view of foraging. First identified in the closely related northern elephant seals, *M. angustirostris* (Crocker et al. 1997) drift dives are characterized by three distinct phases. In

two of them, the initial (descending), and final (ascending) phases, the seal is actively swimming in the water column. During the period in between descent and ascent phases, (the drifting phase) the seal stops swimming and 'drifts' passively through the water column. The speed of this vertical displacement is determined mostly by the buoyancy of the seal, which, ultimately, depends on the fat:lean tissue ratio (Crocker et al. 1997, Webb et al. 1998); typically, lean animals are negatively buoyant and approach neutral buoyancy as they increase their fat reserves, sometimes reaching positive buoyancy. If these drift dives are properly identified, and the drifting rate is calculated, then it can be used to estimate the body condition, and to track changes in seal condition during the two annual foraging trips (Biuw et al. 2003, Thums et al. 2008a, Gordine et al. 2015). Contrary to other approaches to measure foraging behaviour, such as accelerometers traditionally used to infer prey capture events on elephant seals (but see Miller et al. (2004) and, Aoki et al. (2011) for recent use of accelerometers to estimate body condition on other species), the drift rate analysis actually provides a measure of the net rate of energy intake. Specifically, the amount of extra energy intake above the individual metabolic requirements that is accumulated specially in the fat tissue (blubber). Drift rate analysis can therefore be a powerful tool to quantify individual at-sea performance and for determining the relationships between foraging success, individual behaviour, and the environment (Bailleul et al. 2007b, Biuw et al. 2007, Robinson et al. 2010, Thums et al. 2013, Richard et al. 2016). Ultimately, what really matters for a predator is not just how many prey items are caught. Many individual prey catches does not necessarily translate into a higher energy gain, if the energetic value of the prey is low and the hunting costs are high. Rather, of key interest is how much energy is actually being assimilated (net gain) and how this affects survival and reproduction.

Drifting behaviour therefore presents an excellent tool to quantify foraging success, making this species an ideal model for the study of foraging behaviour, especially for marine predators feeding in remote regions of the world's oceans (Bailleul et al. 2007b, Biuw et al. 2007). Importantly when we can retrieve drift dive information along with other behavioural and environmental data, we have a powerful tool to study the behavioural responses to changes in foraging success in real time. In remote areas such as most of the Southern Ocean, where detailed information of the complete food chain, and prey fields is incomplete, we can link the degree of foraging success with the immediate environment, infer which areas of the Southern

Ocean support higher energy transfer towards the upper trophic levels and ascertain the characteristics of these regions.

1.3 Aims and thesis structure

Marine prey fields and actual foraging activity of marine predators is challenging to study. However, because elephant seals drift, we may study individual foraging success using this information as a proxy This thesis aims to 1) firstly develop a robust and reliable quantitative approach to extract drift dives and calculate drift rates throughout foraging trips at sea. This approach will then 2) be used to assess the quality of different Antarctic regions, from the viewpoint of a top predator, with a focus on coastal polynya regions. The last analytical part of the thesis3) uses the direct measures of foraging success (absolute drift rate and changes in drift rate) to address dive optimization within the context of different foraging strategies exhibited by elephant seals.

1.3.1 Tracking the body condition of Southern elephant seals

Chapter 1 develops a novel approach to detect drift dives and estimate the drift rate of southern elephant seals, using dive information as summarized by the broken-stick algorithm used in SRDLs. I first visually inspected and classified ~15,000 high-resolution dive profiles (i.e. comprising time-depth records every 8 sec) from three elephant seals. Once classified (as either drift or non-drift dives), the dives were summarized using a broken-stick algorithm to emulate the onboard SRDLs processing that occurs before transmission through the ARGOS system. Next, I developed and applied a reverse broken-stick algorithm that groups the profiles according to the order in which the inflection points are selected by the algorithm, and whether these are positively or negatively buoyant dives. This grouping allows high flexibility necessary for the subsequent step, in which a set of dive metrics are calculated and compared between drift and non-drift dives, to establish accept-reject thresholds to automatically and efficiently reject non-drift dives. This generates a subset of candidate drift dives. The final step uses a custom Kalman filter to make the final selection of drift dives from the proposed candidates. Kalman filters are a family of statistical techniques developed to process noisy time-series, removing inconsistent or erroneous points. Here, I use it to remove those candidate drift dives that are unlikely to belong to the drifting trajectory of each seal.

Chapter 2 demonstrates ready-to-use software I developed to implement the method detailed in chapter 1. The R statistical language is a free software environment developed for statistical analysis and advanced graphic methods. It is released under the GNU General Public license (the Free Software Foundation), is readily available to most computer platforms, and is fast becoming the standard platform to conduct quantitative ecological research. Besides the core statistical functionality, R is easily extended via contributed packages (currently around 15 000 just in CRAN, see https://cran.r-project.org/). Thus, R was chosen to implement the method, making it easily available to any researcher interested in analyzing the drift rate of southern elephant seals (or their conspecifics, or any other species that perform drift dives). The package *slimmingDive* is currently hosted in GitHub (https://github.com/farcego/slimmingDive) and archived in Zenodo.

1.3.2 Heterogeneity of Antarctic environments from the viewpoint of a marine predator

Chapter 3 Here I build on my findings and use the key analytical tool, the method I developed in chapters 1 and 2, to explore differences of the eastern Antarctic region in terms of movement behaviour and Drift rate of a top predator. Southern elephant seals forage in a diverse range of ocean habitats and recent research has highlighted their usage of Antarctic coastal polynyas (recurrent areas of open water in the sea-ice). This chapter specifically focuses on the importance of coastal polynyas as regions known to exhibit high primary productivity. To examine whether the benefits of this productivity translate into higher energy transfer to upper trophic levels, the study quantifies: (i) the horizontal movement behaviour of elephant seals (inside and outside polynyas) to explore which seals usepolynyas (and to what extent), and (ii) the changes in Drift rate (i.e., the rate of increase in the seals' post-moult body condition) inside versus outside polynyas. I have restricted these analyses to austral summer-autumn. As Winter advances, sea-ice growth may impose further restrictions to seal movements outside polynyas. The potential benefits of coastal polynyas are further discussed in the context of which individuals target polynyas – primarily males – from a life-history perspective.

1.3.3 Behavioural responses to changes in foraging success

Chapter 4 tests whether elephant seals exhibit observable changes in their diving behaviour as a direct response to changes in their drift rate and to enhanced foraging success, under the

assumption that this success is mediated by an enhanced foraging environment. The relationships found between body condition and diving metrics may improve our ability to predict body condition at sea, even during periods when seals are not exhibiting drifting behaviour. It is important to consider the environment in which individuals are foraging, since any behavioural response (if present) likely depends on the prey type being targeted and body condition. Thus, benthic and pelagic diving is treated separately as these imply targeting of different prey fields with different properties. For example, benthic foraging is expected to target large, solitary, benthopelagic fishes, whereas pelagic foraging is likely to be targeting mesopelagic assemblages of fish and squid. In this context, there ought not to be any major advantage to optimize foraging dives during benthic foraging. Being linked to large solitary individuals prey items of scattered distribution along the seafloor. Hence, a modification of their diving behaviour, like the speed of transit from the surface to the seafloor, should not substantially increase their chances to find another prey. However, in the case of pelagic divers some kind of optimization should be expected; here, a fast return to the forage depths could enhance the likelihood of relocating the prey field, which may be hard to find again.

1.3.4 Synthesis and perspectives

Chapter 5 integrates the findings from the data chapters within a wider context, considering broader ecological processes and their interactions with the physical environment. This section synthesizes the significant advance for the current knowledge on this foraging ecology of southern elephant seals, particularly the differences found between sexes / regions, to shed light on the evolution of foraging strategies, life history tactics (like predator avoidance) and breeding strategies. I provide perspectives both under the current but also for future scenarios, for example with respect to the potential impacts of climate change on the accessibility of quality foraging areas.

Chapter 2 A quantitative, hierarchical approach for detecting drift dives and tracking buoyancy changes in southern elephant seals.

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2.1 Abstract

Foraging behaviour of marine predators inferred from the analysis of horizontal or vertical movements commonly lack quantitative information about foraging success. Several marine mammal species are known to perform dives where they passively drift in the water column, termed “drift” dives. The drift rate is determined largely by the animal’s buoyancy, which can be used to make inference regarding body condition. Long term dive records retrieved via satellite uplink are often summarized before transmission. This loss of resolution hampers identification of drift dives. Here, we develop a flexible, hierarchically structured approach to identify drift dives and estimate the drift rate from the summarized time-depth profiles that are readily available to the global research community. Based on high-resolution dive data from archival tags deployed on southern elephant seals, we classify dives as drift/non-drift and apply a summarization algorithm mimicking that used to summarize dives on satellite-linked instruments. We then i) automatically generate dive groups based on inflection point ordering using a ‘Reverse’ Broken-Stick Algorithm, ii) develop a set of threshold criteria to apply across groups, ensuring non-drift dives are most efficiently rejected, and iii) finally implement a custom Kalman filter to retain the remaining dives that are within the seals estimated drifting time series. Validation with independent data sets shows our method retains approximately 3 % of all dives, of which 88 % are true drift dives. The drift rate estimates are unbiased, with the upper 95% quantile of the mean squared error between the daily averaged summarized profiles using our method (SDDR) and the observed daily averaged drift rate (ODDR) being only 0.0015. The trend of the drifting time-series match expectations for capital breeders, showing the lowest body condition commencing foraging trips and a progressive improvement as they remain at sea. Our method offers sufficient resolution to track small changes in body condition at a fine temporal scale. This approach overcomes a long-term challenge for large existing and ongoing data collections, with potential application across other drift diving species. Enabling robust identification of foraging success at sea offers a rare and valuable opportunity for monitoring marine ecosystem productivity in space and time by tracking the success of a top predator.

Key-words Drift dives, foraging success, Integrated Marine Observing System (IMOS), kalman filter, body condition, *Mirounga leonina.*

2.2 Introduction

Foraging is a central element of an animal's life. Being a successful forager is directly translated into survival, reproduction, and ultimately population growth (Stearns 1992). Foraging activity (where, when and how individuals acquire resources), is therefore a core concern that underpins ecological research. Acquiring this information from terrestrial systems is difficult but tractable. However, collecting information on foraging behaviour from marine animals is especially challenging because their oceanic environment limits our ability to make direct observations of feeding activities.

Broadscale approaches to studying the foraging ecology of marine predators include stomach contents (Marshall et al. 2010), stable isotopes (Walters et al. 2014), fatty acid signature (Bradshaw et al. 2003, Banks et al. 2014) and genetic methods (McInnes et al. 2017). Animal telemetry approaches, with the on-going development and miniaturization of sensors, provides increasingly detailed insight into many aspects of marine organisms' ecology (Hussey et al. 2015). Sensors currently devoted to directly studying foraging ecology of marine megafauna include stomach and oesophageal temperature sensors (Bestley et al. 2008, Kuhn et al. 2009), accelerometers capturing head or jaw movements (Gallon et al. 2013, Viviant et al. 2014, Adachi et al. 2016, Jouma'a et al. 2016), as well as *in situ* miniaturised video cameras (Watanabe and Takahashi 2013). However, these approaches typically provide relatively short time-series on foraging behaviour in marine birds and mammals.

More commonly, telemetry-based studies of marine predators have relied on using behaviour to indirectly infer foraging. Generally, movement patterns of individuals are used to infer foraging areas. A broad suite of techniques have been applied to horizontal movements including heuristic methods such as area restricted search (Kareiva and Odell 1987, Fauchald 1999, Fauchald and Tveraa 2003) through to sophisticated process-based methods such as State-Space Models (Morales et al. 2004, Langrock et al. 2012, Jonsen et al. 2013). Research effort has also focussed on inferring foraging behaviour from vertical movements using dive-based indicators (Thums, Michele.J.A, Hindell et al. 2011, Dragon et al. 2012). Nonetheless, direct empirical information on foraging events, and especially evaluating foraging *success*, remains elusive.

An alternative way to evaluate foraging success is to track changes in the animals' body condition. For marine mammals, changes in body condition can be evaluated through buoyancy

changes associated with an increase or decrease in the fat:lean tissue ratio (Biuw et al. 2003). Some marine mammals have been found to perform certain types of "drift" dives made up of three distinct phases: (i) an initial descent phase, when the animal is actively diving to depth, (ii) an inactive "drift" phase, when the animal is not actively swimming, and (iii) an ascent phase, when the animal actively returns to the surface. During the inactive phase, the rate of drifting is mostly determined by the fat:lean tissue ratioof the animal and the surrounding media (Biuw et al. 2003). The total buoyant force acting on an object immersed in water is a function of the object's density relative to the density of the surrounding water, and, in animals also by the effect if residual volume of air filled body cavities such as lungs (Miller et al. 2016, Aoki et al. 2017, Narazaki et al. 2018). Biuw et al. (Biuw et al. 2003) investigated the effect of these parameters, finding only limited effects of salinity, and residual lung air at depths greater than 100 m. This type of dive was initially identified in Southern (Hindell et al. 1991b) and Northern (Crocker et al. 1997) elephant seals, known to be deep divers (Le Boeuf et al. 1988, Arnould and Hindell 2001), but similar drift behaviours have been reported across a range of marine mammals including New Zealand Fur Seals (Page et al. 2005), sperm whales (Miller et al. 2008), hooded seals (Andersen et al. 2014) and Baikal seals (Watanabe et al. 2015). For the shallow diving species the effect of residual air in the lungs may influence the drift rate.

Southern elephant seals (*Mirounga leonina*) are an abundant predator of the Southern Ocean, spending over eight months per year at sea (Hindell et al. 1991b). In between two periods on land, to breed and to moult, the seals travel long distances to forage (Hindell et al. 2016). As capital breeders, southern elephant seals fast during the periods they spend on land, so the energy they rely on for self-maintenance, moulting and breeding must be accumulated while the seals are at sea feeding; importantly it is these resources that are a key element determining individual fitness (Stevenson and Woods 2006). Southern elephant seals store energy in the form of lipids (Fedak et al. 1994) resulting in changes in the individual's buoyancy as fat is accumulated or lost (Biuw et al. 2003). Quantifying these changes in buoyancy can provide an extremely useful index for estimating the net energy gain, i.e., where and how much forage resource seals are acquiring, whilst at sea (Biuw et al. 2003, 2007, Bailleul et al. 2007b, Schick et al. 2013, Gordine et al. 2015, Richard et al. 2016).

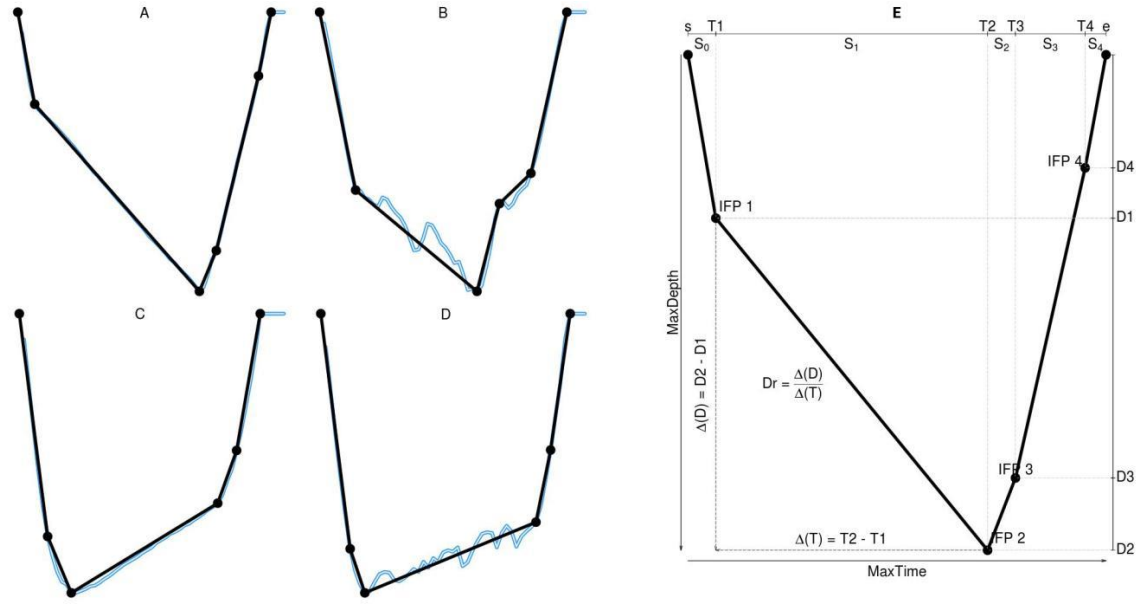


Figure 2.1. Explanation of drift dives obtained from summarized high-resolution tag data. *Example of an (A) negative and (C) positive drift dive, as well as non-drift dives whose summarized forms incorrectly resemble (B) negative and (D) positive drift dives. Blue lines represent high-resolution time depth profiles, while black represents the summarized profiles from the Broken-Stick algorithm. (E) Diagram of a summarized drift dive including the main criteria used to classify summarized profiles as drift dives. For this dive, the ifp (inflection point order) is 2.1.3.4. Summarized inflection points are IFP1{T1,D1}, IFP2 {T2,D2}, IFP3 {T3,D3} and IFP4 {T4,D4}. ps0 represents the proportion of the dive duration spent on the descending phase (T1/MaxTime etc.). S_1 the proportion spent along the first BSA segment (T2-T1 / E), S_2 along the second segment (T3-T2 / E), S3 for the third segment (T4-T3 / E) and S4 between the last ifp and the end of the dive (e-T4 / E). Drift rate (Dr) is calculated as the difference in depth divided by the difference in time over the drifting segment (in this case, the segment between IFP1 and IFP2).*

Generally, dive profiles for determining the presence of drift dives come from high-resolution time-depth recording archival tags (Thums et al. 2008a, Robinson et al. 2010, Richard et al. 2014b, 2016). However, these tags have to be retrieved from the animal in order to access the high-resolution dive data. When these time-depth recorders are integrated into satellite-relayed tags, the data can be recovered in near real time without having to physically access the tag (Fedak et al. 2002, Photopoulou et al. 2015a). The most common way of recovering the dive information of oceanic, long-ranging species is through the ARGOS satellite system (Argos 2011). Despite the overall utility of the Argos system there are constraints on how much information can be received, so detailed time-depth profiles need to be summarized before being

transmitted (Fedak et al. 2002, Photopoulou et al. 2015a). Mostly, time-depth profiles are summarized using a broken-stick algorithm (BSA) (Fedak et al. 2001, Photopoulou et al. 2015b). Although summarizing the data in this manner provides a reliable way of transmitting and receiving information, the reduced detail on the dive shape makes identifying dive types, including drift dives, challenging (Heerah et al. 2014).

Southern elephant seals are regularly tagged with satellite-linked time-depth-recorders across their range in the Southern Ocean. These tags normally carry oceanographic sensors to simultaneously record behaviour and physical hydrography (Charrassin et al. 2008, Gordine et al. 2015, Hindell et al. 2016, Williams et al. 2016). As these tags are seldom recovered, most of the dive behaviour is only available from the summarized profiles transmitted through the Argos satellite system (Treasure et al. 2017). While drift dives can be detected from these (Biuw et al. 2003, 2007, Bailleul et al. 2007b), changing dive profile summarization algorithms after Biuw et al. (2003) developed method have prevented the wide use of these methods based on summarized dive profiles to extract seal body condition . One recent study has proposed a new filtering process applied uniformly to all subsurface segments of summarized dives performed by the seals (Gordine et al. 2015). Here, we build on these approaches and develop a flexible, hierarchically structured approach to identify drift dives and estimate the drift rate from summarized time-depth profiles that are increasingly available to the global research community ((Treasure et al. 2017) and references therein). In developing this new method we i) automatically generate dive groups based on a 'Reverse' Broken-Stick Algorithm (RBSA), ii) apply filters with threshold characteristics tuned for each group, ensuring non-drift dives are most efficiently rejected, and iii) finally implement a custom Kalman filter to retain the remaining dives that are within the seal estimated drifting time series. Compared with available methods (Gordine et al. 2015), our approach is not solely based on a set of fixed criteria applied uniformly to all dive segments. Rather, we first generate a set of candidate drift dives, automatically grouped, allowing us to create a set of thresholds for each group. This makes our approach more flexible in terms of coping with diving heterogeneity. We apply these thresholds to specific groups of dives, rather to any diving segment. Our approach contributes to overcoming the long-term challenge for large existing and ongoing data collections which contain only summarized dive profiles, enabling robust identification of foraging success at sea with potential application across other drift-diving species. This will provide the basis for

biological and environmental drivers of spatial and temporal patterns in feeding success to be further explored, a unique and rare opportunity in marine systems.

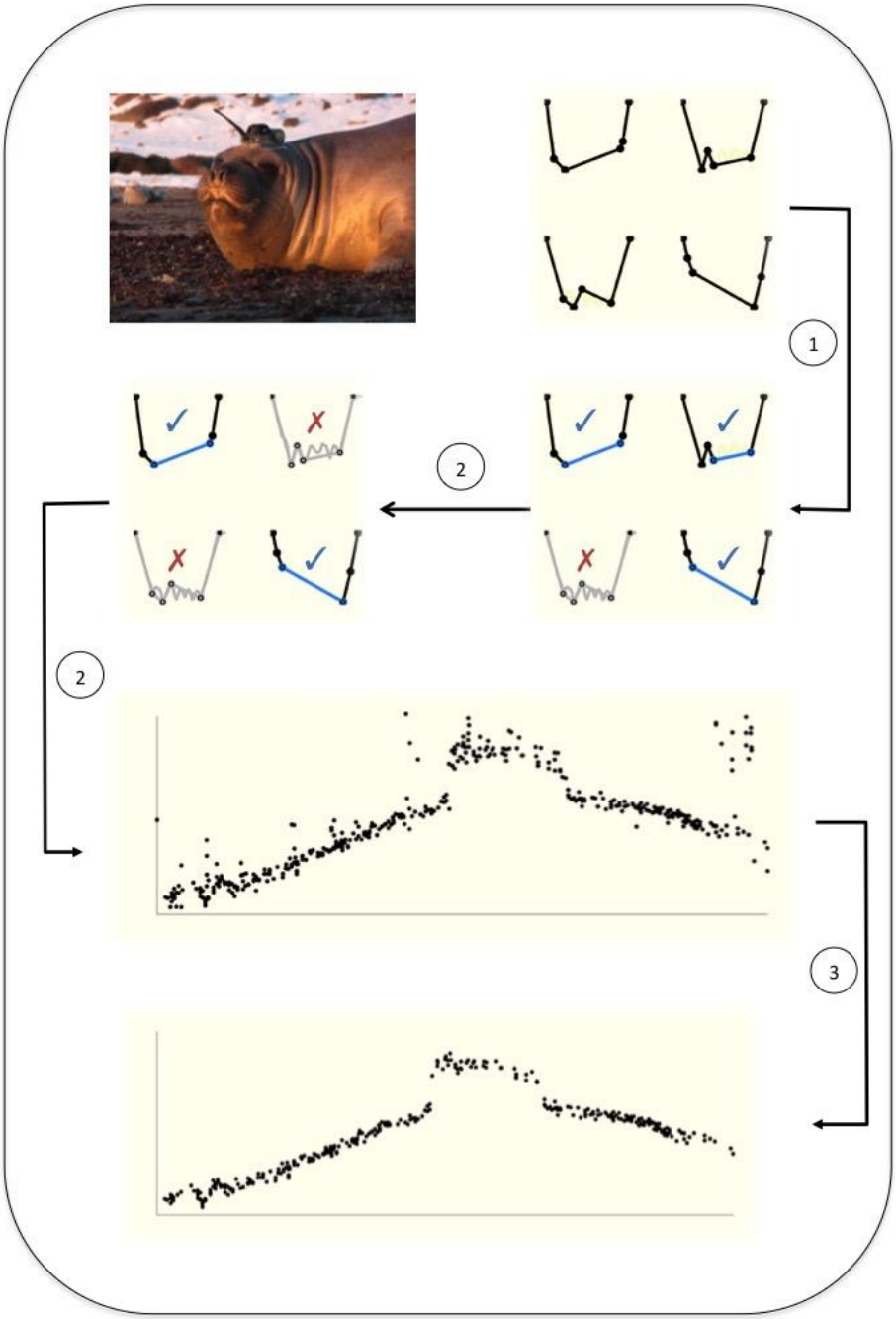


***Figure** 2.2. Conceptual diagram representing the drift dive methodology**: i. Seal is instrumented and summarized dive profiles are transmitted; ii.1. Using the Reverse Broken-Stick Algorithm (RBSA), dives are grouped according to inflection point ordering and candidate groups of drift dives identified. At the same time, the putative drift segment is assigned (blue);*

ii.2. A set of threshold criteria are applied to each candidate group to further isolate certain drift dives (red crosses indicate rejected dives, and blue ticks accepted dives), however visualization of the observed drift rates reveals some noise remains in the drift trajectory; iii: The custom Kalman filter is applied to the drift rate observations to obtain the final drift rate trajectory over time. Seal picture © Fernando Arce.

741 # 2.3 Materials and methods

742 ## *2.3.1 Tag data and processing*

743 In developing our method to identify drift dives and estimate drift rates from summarized dive
744 profiles, we first utilised high-resolution dive records. We randomly selected three high-
745 resolution time-depth series from a set of Macquarie Island (50° 30' S, 158° 57' E) deployments
746 on southern elephant seals during 2004. All tags were velocity-time-depth recorders (VTDR,
747 Wildlife Computers MK8, Redmond, Washington, USA) sampling depth and velocity at 30 s
748 intervals. Tags were attached to adult females; two during post breeding and one during the post-
749 moult trip. Se Field et al. (2002) and McMahon, Field, Bradshaw, White, & Hindell (2008) for
750 seal instrumenting procedures. Seal instrumentation was carried under ethics approval form the
751 Australian Antarctic Animal Ethics Committee (AAS 2265 & AAS 2794) of the Australian
752 Antarctic Division.

753

Seal id	*Trip*	*Dives*	*Drift dives*			
			Certain	*Uncertain*	*Positive*	*Negative*
b14304pm	pm	10913	703 (6.4%)	180 (1.6%)	178 (1.6%)	525 (4.8%)
c06404pb	pb	3879	179 (4.6%)	19 (0.5%)	0 (0%)	179 (4.6%)
c09004pb	pb	2830	190 (6.7%)	51 (1.8%)	0 (0%)	190 (6.7%)
Total		17622	1072 (6.1%)	250 (1.4%)	178 (1.0%)	894 (5.1%)

Table 2.1. Number of high-resolution time-depth recorder (TDR) dives used for the development of the drift dive methodologies. *Shown are the numbers of dives visually classified as drift dives; either as certain or uncertain. Certain drift dives are indicated as positive (i.e. upward drift segment) or negative (i.e. downward drift segment). Trip types are indicated as post-moulting (pm) or post-breeding (pb). Numbers in parentheses give percentages.*

From all the dives (n=18064) recorded by the tags, we only kept those dives reaching a minimum depth of 100 m, to avoid potential bias from residual air in the lungs. We also removed those dives with a duration lower than 300 sec as they are short, shallow, exploratory dives (Biuw et al. 2007, Thums et al. 2008a, 2008b). That resulted in a final set comprising 97.5% of the original dives (n=17622, Table 2.1). We visually inspected all dives meeting these criteria and classified them as potentially drift or non-drift dives according to their shape and the velocity records; potential drift dives requiring a passive ascent or descent phase, without directional changes ("wiggles") (Fig. 2.1) or abrupt changes in the recorded velocity. Drift dives were further allocated as certain or uncertain, and as positive or negative. We then summarized each high-resolution VTDR dive using a Broken-stick algorithm (BSA). This reproduces the on-board processing of dives that occurs on the SRDLs (Fedak et al. 2001, Photopoulou et al. 2015b), resulting in a summarized form with only four subsurface inflection points retained together with the start and end points (Fig. 2.1).

2.3.2 Drift dive selection process

For the automated drift dive selection process on the summarized dive profiles, we introduce two new important steps. First, we pay particular attention to the order in which the inflection points are selected by developing a 'Reverse' Broken-stick algorithm (hereafter RBSA), similar to a recently implemented approach (Photopoulou et al. 2015b) which aids in grouping candidate drift dives. Secondly, we develop a set of threshold criteria with respect to dive profile characteristics to apply across groups, to automatically select those dives whose drift rates will be submitted to the final Kalman filtering stage.

2.3.2.1 Reverse Broken-Stick algorithm (RBSA)

The RBSA generates the order in which the inflection points are selected before the satellite transmission. The RBSA recreates the steps taken onboard the SRDLs . From the summarized profiles the only inflection point whose original position is known is the deepest point, that is, the first selected point (as it shows the highest difference between the original high-resolution time-depth profile and the surface). A linear profile is constructed between this deepest point and the start and end points of the dive. The second point will then be determined by the largest discrepancy between the linear profile and the transmitted points. The RBSA recursively reconstructs the profile until the fourth and final point is found (Photopoulou et al. 2015b). The

RBSA also generates the original residuals from the BSA the last of which, *i.e.* the largest remaining difference between the summarized and detailed profile, gives a relative indication of the amount of vertical activity not well captured by the summarized profile.

The inflection points are transmitted sorted by time of occurrence along the dive, not by the order in which they are selected by the BSA. Thus, an inflection point order of [2.1.3.4] indicates that the first point selected by the BSA will be the second timestamp (T2, D2) of the dive profile, the second inflection point selected is the first timestamp (T1, D1) and so on. This inflection point order (ifp) is used to organise the dives into groups.

The distribution of known (certain) drift dives from the high-resolution VTDR data was checked across these RBSA groupings, and used to make a first pre-selection of candidate drift dives (i.e. those dives that may be drift dives). Of the possible 24 groups identified by the inflection point ordering, eight comprised the majority of the known drift dives (> 90 % total). These groups became the only ones considered as potential drift dives (step 1, Fig. 2.2) and retained for the following calculations and selection procedures.

2.3.2.2 Drift rate estimate

A combination of different dive proportions and the position of the deepest point are then used to determine the drift segment of each potential drift dive (Appendix 2.A and Table 2.2). Drift rate ($m\ s^{-1}$) is then calculated as the difference of depth between the start and end point of the drift segment with respect to the time spent on the segment, i.e. $Dr = \Delta(D)/\Delta(T)$ (see Fig. 2.1). The sign of the drift rate allows us to further allocate dives into negative/positive subgroups. All drift rates throughout the chapter have units of $m\ s^{-1}$.

2.3.2.3 Developing threshold criteria

For each individual dive profile, a number of numerical variables were calculated based on dive proportions. Proportional values were used to scale variables irrespective of shorter/longer or shallower/deeper absolute profiles, to minimize the influence of seals diving variability. Figure 1 provides a visual aid for these variables, which each give information about the dive shape, and a detailed description of the threshold criteria is provided in Appendix A. For each dive group we separately constructed density plots of these variables for both certain drift and non-drift dives,

allowing different threshold criteria to be developed and automatically applied across the different groups (step 2 in Fig. 2.2).

The criteria selection and its thresholds for each group were developed sequentially as follows:

First, density plots of all the proposed criteria for each seal were constructed, to show the degree of overlapping for drift and non drift dives. The criterion with the lowest degree of overlap was then selected first. This selected criterion was inspected in greater detail with an accepting-rejecting plot (see Appendix 2.A) to find an optimal threshold; aiming for a reduction of ~50% of the non drift dives at a cost of losing as much as 5-10% of the true drift dives. Once the first threshold was identified, it was applied to the dataset, and the previous step was iterated for each of the 15 groups until no further optimal threshold could be found.

2.3.3 Kalman filtering drift rates

The two-step process described above supplies a final set of candidate drift rates to a custom Kalman filter. This is implemented to remove those dives with unrealistic drift rates in relation with the seal drift time series. Step 3 in Figure 2 gives a schematic representation of the filtering process. Kalman filters are a family of methods used to filter time series and reject/recalculate points using the trajectory of the signal, for example to filter noisy animal movement paths (Sengupta et al. 2012). We applied the Kalman filter to the drift rate time series of each individual animal. Our Kalman filter assumes that (i) the vertical drift rate of a seal is proportional to the squared root of the difference between water density and the seal body density, (ii) water density is constant, and (iii) seal density changes through mass accretion (primarily blubber), and takes the general form:

$$\rho_k = \frac{m_0 + \delta_k}{v_0 + V\delta_k}$$

$$\mu_k = \alpha sign(\rho_k - 1)\sqrt{\rho_k - 1\,\mathrm{v}}$$

where:

ρ_k = seal density at dive k

m_0 = initial mass (Kg)

$$\delta_k = massincrement$$

v_0 = initial volume

$$V\delta_k = incrementofvolumeassociatedwiththemassincrementatdivek$$

$$\mu_k = buoyancyofthesealatdivek$$

$$\alpha = constant$$

$$sign(\rho_k - 1) = signoftheseal'sdensity$$

$$calculation$$

$$\sqrt{|\rho_k - 1|} = squaredrootofthedifferencebetweensealdensity \wedge water$$

$$densityatdivek$$

We then modelled the mass increments δ_k as a random walk:

$$\delta_k = \delta_{k-1} + \eta_k$$

$$\eta_k N\left(0, \tau^{(\delta)}/(t_k - t_{k-1})\right)$$

where:

$$\delta_k = massincrementatdivek$$

$$\delta_{k-1} = massincrementatdivek - 1$$

$$\eta_k = variationonthemassincrementassociatedwiththedivek$$

$$\tau^{(\delta)} = varianceof\eta_k dependentonthemass$$

$$(t_k - t_{k-1}) = timeincrementbetweenthecurrentdive \wedge thepreviousone$$

and we consider the error on the drift rate observations as normally distributed:

$$r_k N\left(\mu_k, \tau_{z_k}^{(r)}\right)$$

where:

$$r_k = observeddriftrateforthedivek$$

$$\mu_k = buoyancyofthesealatdivek$$

862 $$\tau_{z_k}^{(r)} = varianceontheobserveddriftrateconditionedonwhether \vee notdive$$

863 $$kbelongsthetrajectory$$

864

865 The initial condition at time zero is determined by the first candidate Drift dive. The Kalman
866 filter evaluates whether any drift rate observation associated with the time-varying density
867 change process is inside or outside the most likely trajectory of the time series based on the
868 expected variation associated with both the process and the observation. Whether any potential
869 drift dive is inside or outside the trajectory of the drifting time series is defined as a binomial
870 state variable Z_k with two possible outcomes: 1 (dive k is inside the trajectory) or 0 (dive k is
871 outside the trajectory):

872 $$z_k Bin(1, p)$$

873 The most probable drift rates of observations that are unlikely to be inside the trajectory of the
874 drifting time series may also be estimated. However rather than using the estimated drift values,
875 we accept as drift dives only those with a probability of being inside the trajectory close enough
876 to 1 [$P(Z_k = 1) > 0.95$] and retain these observed drift rates.

877 ## *2.3.4 Validation of the method*

878 ### *2.3.4.1 Drift rate evaluation*

879 To obtain the "true" drift rates we computed the rate of change in depth for all time-steps inside
880 each drifting segment from the original high-resolution time-depth records. To check the
881 robustness of our final drift rates the median of all these values was then subtracted from the
882 value extracted from the summarized dive profile as a measurement of bias.

883 We also generated an observed daily averaged drift rate (ODDR) from the high-resolution drift
884 dives. These were compared with a daily averaged drift rate calculated from the summarized
885 profiles using our method (SDDR), and the difference between both used as another direct
886 measure of bias.

887 To quantify the improvement in estimations due to the Kalman filter we calculated the SDDR
888 before and after the application of the Kalman filter. We compared the performance by
889 calculating the squared error and its mean (msr) between both SDDR's and the ODDR.

2.3.4.2 Validation with independent seal data

To assess our model performance, we processed six additional data sets from Macquarie Island deployments during 2004 post-breeding trips as well as four from 2005 post-moulting trips (n = 10 seals). We visually inspected the high-resolution profiles of those dives accepted by our hierarchical procedures and calculated the proportion that were true drift dives.

All the filtering procedures have been implemented in R (R Core Team 2018) and JAGS (Plummer 2003) and are freely available in the form of an R package (https://github.com/farcego/SlimmingDive)

2.4 Results

From the 17622 high-resolution dive profiles visually classified, 1072 (6.1%) and 250 (1.4%) were classified as certain or uncertain drift dives, respectively (Table 1). Seal b14303, undertaking a post-moult trip, was the only one with identifiable certain positive drift dives, with a proportion of 4.8% and 1.6% for negative and positive drift dives respectively (Table 1). We found an average of 5.1% (range 4.6-6.7%) of certain negative drift dives across the three seals (Table 1). These numbers are consistent with previously reported values from this dataset [39].

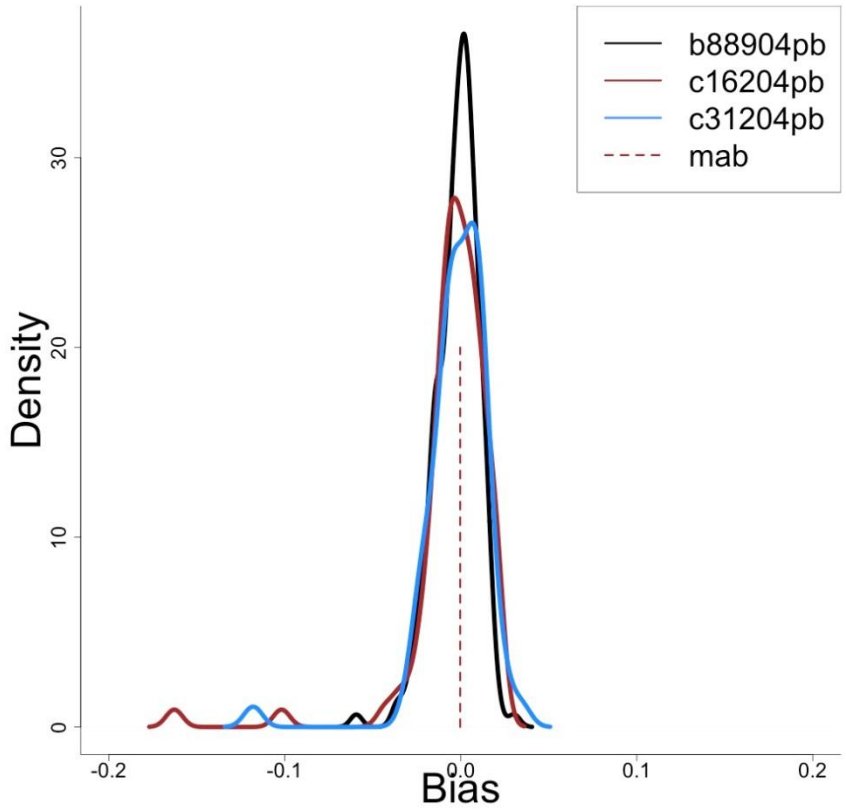


Figure 2.3. Drift rate evaluation. Density plot shows the bias calculation for the final drift rates (m/s) obtained using summarized profiles relative to the "true" drift rates obtained from high-resolution data. Curves are shown for the three processed seals (n = 735, 191 and 200 drift dive observations), together with the median averaged bias (mab = -0.0003).

2.4.1 Drift dive selection process

Upon application of the RBSA, we retained eight major dive groups as candidate drift dives with the following inflection point (ifp) orders: [2.1.3.4, 2.1.4.3, 2.4.1.3, 3.1.2.4, 3.1.4.2, 3.2.1.4, 3.4.1.2 and 4.2.1.3]. This removed 3909 out of the 17622 dives, of which only 121 were considered certain drift dives i.e., a low (3.1%) overall false rejection rate (Appendix B). The eight retained groups together represented more than 90% of the certain negative drift dives and 86% of the certain positive drift dives (Appendix B). The criteria developed to automatically determine the drifting segment for each of the eight retained dive groups are shown in Table 2. As an example, for group [2.1.4.3] if the proportional dive time occupied by the first descendent segment is above 0.25, this comprises the drift segment; otherwise the drift segment comprises the next longest segment.

For each group, up to seven threshold criteria were applied sequentially to give a criteria-threshold combination that efficiently rejected certain non-drift dives. The specific criteria applied to each dive group and their threshold values are reported in Table 3. Positive drift dives occurred throughout all major groups, excluding [3.2.1.4] which represented only negative drift dives, and different criteria were applied between positive and negative drift dives within groups (Table 3). An example of a widely applied criterion is *d1*, the ratio between the depth of the first inflection point and the maximum depth, which for known drift dives was less than 0.6 to 0.8 across all groups. The exception was group [3.2.1.4] in which the drift segment is always segment 2 so this threshold (0.8) applies instead to the *d2* criteria. After the application of the threshold criteria, 615 out of 17622 (i.e. 3.48%) candidate drift dives were retained for the Kalman filtering step.

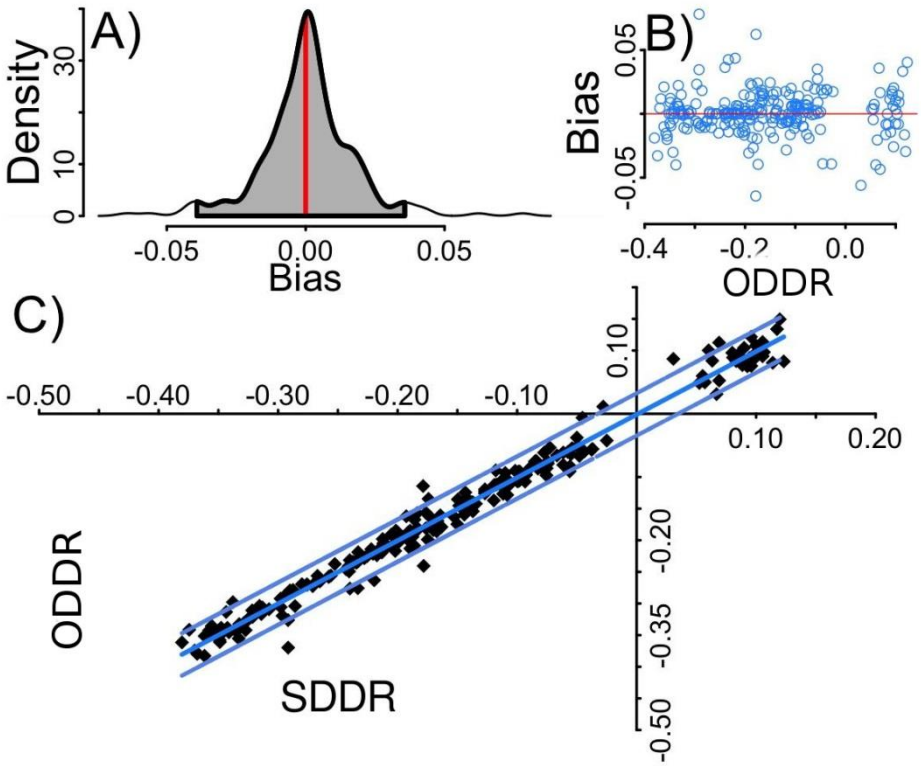


Figure 2.4. Validation of the method. (A) The density distribution of the calculated bias between the daily averaged drift rate from summarized data (SDDR) and the observed daily averaged drift rate (ODDR) for the three seals. Grey shadowed area covers the 95% confidence interval, and vertical red line is drawn at the median. (B) The calculated bias versus the ODDR, evidencing a lack of any trend (horizontal red line set at Y= 0). (C) The positive linear

relationship between the ODDR and the SDDR and the 95% confidence interval (SDDR = -0.001 + 0.986ODDR, r^2= 0.984). All drift rates shown have units of m s^{-1}.

2.4.2 Validation

Application of the Kalman filter rejected 155 (28.2 %), 57 (34.1 %) and 66 (37.3 %) of the final candidate drift dives for the three test seals. The comparison of our final post-filter drift rates with the "true" rates calculated from high-resolution profiles showed there were no differences in the bias distribution among the three seals (F_{238} = 0.3893, p = 0.6778, Fig. 3). The median bias after pooling the three bias distributions across the three seals was -0.0025 (S.D: 0.07, 95% confidence interval (CI): -0.03, 0.02).

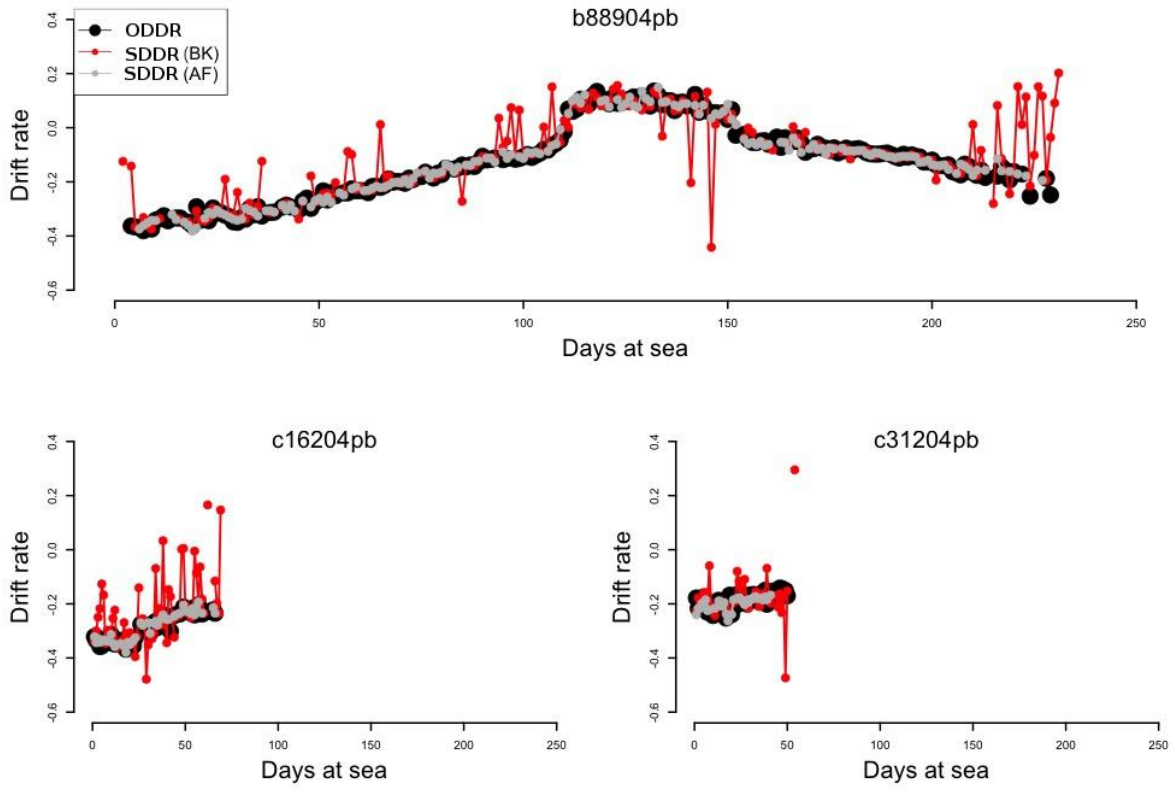


Figure 2.5. ***Kalman filter application.*** *Comparison shows three daily averaged drift rate trajectories of the seals used to develop this method (b88904pb, c16204pb and c31204pb). ODDR refers to the observed daily averaged drift rate and SDDR to the daily averaged drift rate from summarized data both before (BK) and after (AK) applying the Kalman Filter. Lines between points join consecutive daily estimates.*

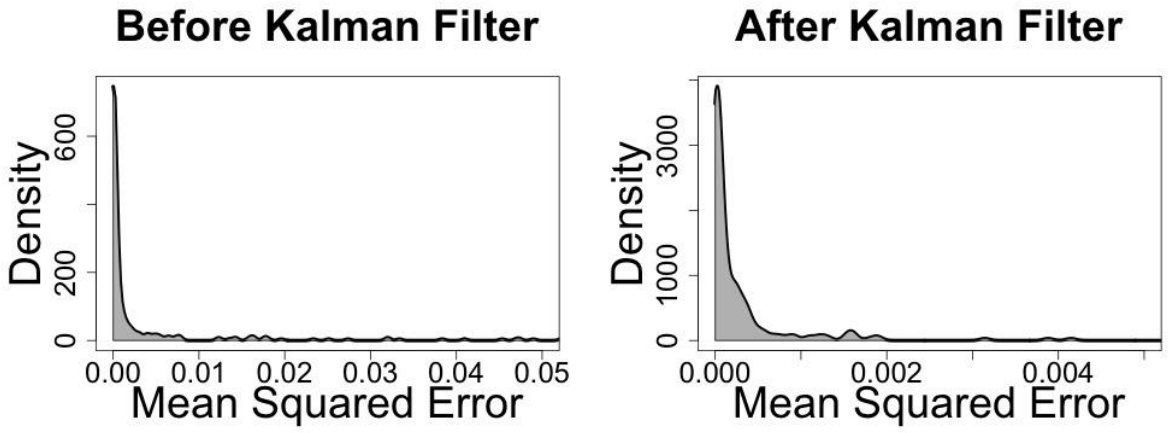
Based on the comparison between the observed daily averaged drift rate (ODDR) and that obtained using our method for summarized profiles (SDDR) there were also no differences in the

939 bias values across the three seals (F_{238} = 2.61, p = 0.08). Once pooled the median value for the
940 bias did not depart significantly from 0 (median: 0, S.D: 0.02, 95% CI: -0.001, 0.002; t_{238} = 0.58,
941 p = 0.56; Fig. 2.4-A). There was no evidence for any trend in bias magnitude associated with an
942 increase in the theoretical daily averaged drift rate (r = 0.02, t_{238} = 0.33, p = 0.74; Fig. 2.4-B).
943 The correlation between the ODDR and SDDR daily averaged drift rates (r = 0.99, p < 0.001;
944 Fig 4-C) indicates our method was highly successful for the test seals.

945 After applying the Kalman filter, the SDDR time series efficiently followed the ODDR on all
946 three test seals (Fig. 2.5). The Kalman filter implementation substantially reduced the mean
947 squared error between the SDDR and the ODDR by an order of magnitude (95% upper CI before
948 and after being 0.04 and 0.0015, Fig. 6).

949 The validation of our approach with 10 independent seals showed on average the percentage of
950 retained dives being true drift dives was 87.5% (S.D: 9.35, Table 4).

951 The full filtering process is applied across the test (n=3) and validation (n=10) seals is visualised
952 in Appendix C.



953

Figure 2.6. ***Kalman filter performance.*** *Mean squared error (msr) between the summarized daily drift rate (SDDR) and the observed daily drift rate (ODDR) across all observations (n = 1126). (A) before the use of the Kalman Filter (mean ± SD = 0.005 ± 0.014 , upper 95% CI = 0.04), and (B) after the Kalman Filter's application (mean ± SD = 0.0002 ± 0.0006, upper 95% CI = 0.0015). Note the order of magnitude reduction on the x-axis scale in (B).*

2.5 Discussion

The occurrence of drift dives, where animals passively sink or rise in the water column, enables buoyancy changes to be estimated in some marine species. Drift rate changes related to changes in relative body composition provide a rare and valuable index of foraging success at sea. Here, we have presented a reliable method to quantify drift rates from the summarized satellite relayed time-depth-record data widely used for migratory marine species. The process-based Kalman Filter is consistent with our understanding of the ecological processes governing the energy budgets of elephant seals i.e. a gain in fat during the two at-sea phases of the seals annual cycle, with effective results for both post-breeding and post-moult animals. We have not directly considered the effects of residual air as a potential source of bias on our estimates because i) we don't consider shallow dives (i.e. less than 100 m depth) as potential drift dives, and ii) elephant seals exhale before diving. Previous research (Biuw et al. 2003) evaluated the potential effect of residual air present in elephant seal lungs, finding little effect on deep dives. That may not be the case for other shallower, breath-holding marine mammals, where these assumptions may be too strong. Our method overcomes a long-term challenge to robustly identify at-sea foraging success, and provides great opportunity for linkages between ecology, physiology, behaviour and environmental drivers to be further explored.

The new method provides a time series of drift rates, and the daily averaged values we obtain from the summarized dive profiles show good concordance with those obtained from visually inspected high resolution dive profiles. Compared with the existing approach (Gordine et al. 2015), which reported 71.4% of retained dives as being true drift dives, our approach retained 87.5%. That gives over a 15% increase in the true drift rate retention, reducing the impact of false positives on the estimated drift rate time series, and contributing to reduce the error/variance of the estimation.

Inclusion of false positive drift dives can result in a higher variance among drift rate estimates and require some further processing; often achieved with smoothing/interpolating techniques such as splines (Biuw et al. 2003, Thums et al. 2008b, Gordine et al. 2015). Such smoothing/interpolating techniques are based on purely statistical approaches, without any biological process underpinning them. Using a custom Kalman filter incorporates a biologically relevant mechanistic model. Although this filter does not remove every non-drift dive, it greatly

reduces their occurrence to approximately 10% of the final set of retained dives. The filter also reduces the variability of the daily drift rate estimates, by over an order of magnitude (Fig. 5) because any accepted non-drift dive (false positive) has to be consistent with the drifting time series of the seal.

An important improvement from previous approaches is that our method can detect when the seal is positively buoyant. Positive buoyancy has implications for quantifying the individual foraging behaviour and success of individuals, as well as the quality of the foraging grounds. In our study, we have processed five post moulting trips, of which three exhibited substantial periods of positive buoyancy up to 150 days, Compiling a realistic record of daily body condition changes would have not been possible with previous approaches which is the ultimate goal of our approach. We make our method available to the research community in the form of an R package under a General Public License.

The results are also consistent with expectations regarding the energy budgets of seals (Biuw et al. 2003, Thums et al. 2008a, 2008b). All the seals exhibit their lowest body condition at the early part of the foraging trip, after fasting for 1- 2 months (Appendix C). They show a progressive increase of body condition as they remain at sea, indicating that they are foraging sufficiently well for their growth and physiological needs and to gradually replenish their lipid reserves. In the longer post-moult time-series periods of positive buoyancy occur, often followed by a return to negative buoyancy.

Once buoyancy changes at temporal scales of days to months for individual animals can be estimated these data can be used to relate patterns of individual foraging success to factors such as such as who lives or dies, or who pups successfully, and how this links to where (spatially) and how (functionally) individuals may forage. Compiling patterns of foraging success across individuals will facilitate population level studies such as why some populations are stable and others declining (McMahon et al. 2003, 2005b, 2005a). Southern elephant seals have been tagged from all Southern Ocean breeding populations (Hindell et al. 2016), a global effort spanning more than two decades. Many hundreds of individual animals have been tagged, including both sexes as well as adults and juveniles (Field et al. 2005b). Our automated approach is tractable for analysing existing and ongoing large dataset collections for larger overarching studies for example that link performance at-sea to key life-history traits such as survival and

reproduction. To date this has been has been difficult given some of the limitations of the analytical tools available to the community.

Marine predators live in a highly heterogeneous seascape, requiring them to make decisions about where to go for their different life activities (e.g. foraging, breeding). Elephant seals are generalist consumers of a wide array of mesopelagic fishes, squid and crustaceans (Bradshaw et al. 2003) and the decisions individuals make are likely to be sex-dependent (Labrousse et al. 2015), change ontogenetically (Field et al. 2005a, 2007a, 2007b, Bailleul et al. 2010a) and vary regionally (Bradshaw et al. 2003, Hindell et al. 2016). Estimating daily changes in body condition are useful for enquiries at a patch-scale, i.e., decisions such as whether to leave a patch in relation to foraging success (Charnov 1976, Thums, Michele.J.A, Hindell et al. 2011). At a broader scale (regional or basin-scale) we can now directly examine changes in behaviour and performance due to environmental conditions, using covariates recorded either onboard the same tags (i.e. temperature, salinity; e.g. (Bestley et al. 2013)) or synoptic information available from satellite sensors and oceanic models (Bailleul et al. 2007b, Charrassin et al. 2008, Guinet et al. 2014). As Southern Ocean predators, their foraging success can give an integrated (over time and across space) indication of relative quality of the regions in which they forage (Biuw et al. 2007). Patterns in body condition can be used to evaluate the spatial distribution of prime foraging areas and their change in response to environmental conditions (Bailleul et al. 2007b, Biuw et al. 2007, Guinet et al. 2014). Such a robust metric affords the opportunity to directly pursue ecological questions linking animal ecology, behaviour, physiology and environment.

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Author contribution: F. A., S. B., M. A. H., C. R. M and S. W. contributed to the design and development of the work. F.A. and S. W. developed and code for the analysis. F.A. wrote the manuscript with substantial contributions from S. B., M. A. H., C. R. M and S. W.

Code and data accessibility: Available at **https://github.com/farcego/slimmingDive/**

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Table 2.2. Eight main RBSA groups identified by the inflection point ordering which comprised the majority (90.5%) of drift dives. The criteria shown are those used to determine the drifting segment of the candidate drift dives within groups. All dives of the 3.2.1.4 group have the same drifting segment (segment 2) so no criteria is required to determine it. {f,s,t} are the change of depth with respect to time for the first, second, and third segments (excludes the initial/descendant, and last/ascent segments).

order		Drifting segment	
	1	**2**	**3**
2.1.3.4	mdepthbias > 0	mdepthbias < 0	
2.1.4.3	ps1 > 25	ps1 ≤ 25 & (1.1×ps2) ≥ ps3	ps1 ≤ 25 & (1.1×ps2) < ps3
	mdepthbias < 0 & ps1 > ps3		
2.4.1.3	*or*	mdepthbias > 0 & ps1 ≤ ps2	mdepthbias < 0 & ps1 ≤ ps2
	mdepthbias > 0 & ps1 > ps2		
3.1.2.4	avratio < 0	avratio > 0	
		ps1 < 25 & s <0 & t > 0	ps1 < 25 & s > 0 & t < 0
3.1.4.2	ps1 > 25	*or*	*or*
		ps1 < 25 & s < 0 & s < 0 & hp2 > hp3	ps1 < 25 & s < 0 & s < 0 & hp2 < hp3
3.2.1.4		All	
3.4.1.2	mdepthbias > 0 & ps1 > ps2	mdepthbias > 0 & ps1 < ps2	mdepthbias < 0

4.2.1.3	mdepthbias > = 0		mdepthbias < 0

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Table 2.3. Threshold values for dive-based criterion applied to the eight main RBSA groups. Only the cells of the criteria applied contain values. Values in brackets represent the lower (left) and upper (right) open thresholds of the threshold acceptance interval. Dive sign indicates criteria applied to negative (-) or positive (+) drift dives within groups. For full criteria description see Appendix A. In brief: {d1, d2, d3, d4} = ratio between the depth of the first, second, third and fourth inflection points and the maximum depth. {ps1, ps2, ps3} = proportion of the dive duration spent on the first, second, and third segments generated by the RBSA. sratio = ratio between the vertical rate of the descending phase and the vertical rate of the first segment post-descent. meand = mean value of {d1, d2, d3, d4} described above. sdd = standard deviation of {d1, d2, d3, d4}. {r1, r2, r3, r4} = residuals obtained by fitting a least square linear regression through the four inflection points {D1, D2, D3, D4}. mrratio = ratio between the smallest BSA residual and the maximum depth. mdepthbias = difference between the time at maximum depth and half of the total dive duration. mdepthr: ratio between the averaged depth of the inflection points {D1, D2, D3, D4} and the maximum depth. {t1, t2, t3, t4} = ratio between the time of each inflection point and the dive duration.

RBSA order	**2.1.3.4**		**2.1.4.3**		**2.4.1.3**		**3.1.2.4**		**3.1.4.2**		**3.2.1.4**	**3.4.1.2**		**4.2.1.3**	
Dive sign	-	+	-	+	-	+	-	+	-	+	-	-	+	-	+
t1		(0.7, 0.14)	< 0.14	< 0.15	< 0.14	< 0.14	< 0.14	< 0.14		< 0.12		< 0.14	< 0.12	< 0.9	< 0.8
d1	< 0.8		< 0.7		< 0.6	< 0.8	< 0.6	< 0.85	< 0.8			< 0.8		< 0.8	
d4			< 0.8	< 0.6		< 0.8		< 0.7	< 0.8			< 0.8	< 0.8	< 0.8	
mrratio			< 0.15	< 0.2		< 0.15				< 0.3	< 0.2	< 0.2		< 0.2	
ps1	> 0.4		> 0.4		> 0.4		> 0.4	< 0.15	> 0.4						
t4		> 0.9								> 0.9			> 0.85	> 0.85	> 0.8

mdepthr						(0.6,1.4)		(0.8,1.5)		(0.8,1.3)					(0.8, 2)
sratio	< 10								< 10				(2,7)		
ps2								> 0.4		> 0.2	> 0.45				
ps3												< 0.2			
sdd		(0.13, 0.4)								(0.1, 0.3)					
r1						< 0							< 0		
r4		< 0													
mdepthbias				< 0											
meand						< 0.8									
d2											< 0.8				

Table 2.4. Validation of the drift dive methodology with 10 independent Macquarie Island seals. Seal id = reference code for each individual tag/seal. Trip: pb = post-breeding trip, pm = post-moulting trip. N = Total number of dives recorded by each tag. Rd = number of retained dives after the application of our method. %d = proportion of dives retained from the total number of dives recorded. Rdd = number of retained drift dives. %Dd = proportion of the retained dives that were true drift dives, as determined by visual inspection of all retained dives using the original high resolution time-depth profiles.

seal id	*trip*	*N*	*Rd*	*%d*	*RDd*	*% Dd*
b88904pb	pb	4376	72	1.65	66	93.05
c16204pb	pb	6287	87	1.38	86	98.85
c31204pb	pb	5848	68	1.16	61	89.7
c69904pb	pb	2867	197	6.87	180	91.37
c79004pb	pb	4828	80	1.66	68	85
h28504pb	pb	3921	64	1.63	60	93.75
c16305pm	pm	11159	240	2.23	160	66.66
f99305pm	pm	10034	220	2.27	171	77.72
h23305pm	pm	12331	732	6.09	717	97.95
h83305pm	pm	10011	268	2.74	225	83.95
Total		77179	2246	2.82	1972	87.8

2.8 Appendix A: Development and application of threshold criteria

Candidate drift dives are grouped according to the order in which the inflection points are selected, identified by application of a 'Reverse' Broken stick algorithm (8 groups, allocated as positive/negative subgroups, see Methods and Table 3). This Appendix provides information on the development of the set of threshold criteria with respect to dive profile characteristics to apply across groups, to automatically select those dives whose drift rates will be submitted to the subsequent Kalman filtering stage.

2.8.1 *Description*

The threshold criteria to select drift dives are based on dive proportions generated by studying the general shape of drift dives. Figure 1 in the main text provides a visual aid to the dive segments and variables referred to. The full list of dive variables used to develop threshold criteria are:

BSA depth ratios (d1, d2, d3, d4): ratio between the depths of the first (d1), second (d2), third (d3) and fourth (d4) inflection points and the maximum depth, i.e. d1 = D1/MaxDepth etc.

This ratio generates a measure of dispersion of the BSM points with respect to the maximum depth. Their relationship depends on the shape of the dive. In negative drift dives, the ratio of the start point of the drift segment should not be one (or close to) as the seal must keep descending due to its negative buoyancy (maximum depth should be reached at the end of the drifting segment). For positive drift dives, the ratio of the end point of the drift segment should again not be close to one. The seal is expected to have reached the maximum depth before starting to drift upwards, and as the seal is ascending the water column during the drift phase; the depth at the end of the drift segment should be shallower than the maximum depth.

meand: mean value of the four BSM depth ratios (d1, d2, d3, d4)

The mean value of the depth ratios should not be close to one. As the drift segment should start (positive drift dive) or end (negative) at or close to the maximum depth, and will cover the smoothest part of the dive trajectory (i.e., least variation in depth

over time), the rest of the inflection points contain the complexity of the dive activity, which should not occur close to the maximum depth.

sratio: ratio between the vertical rate of the descending segment and the vertical rate of the first segment post-descent, i.e. $[\Delta(D_1)/\Delta(T_1)] / [\Delta(D_2)/\Delta(T_2)]$.

For negatively buoyant seals drifting during the first segment, values lower than 1 are rejected; because, it is not expected for an animal to exhibit an active descent with a rate of depth change slower than occurs during the drift segment. This ratio should also depart from 1, since this would point to a 'V' shaped dive. On the other hand, values too high are characteristic of a flat post-descent segment, typical of 'U', or square-bottomed dives.

sdd: standard deviation of the four BSM depth ratios (d1, d2, d3, d4).

The standard deviation of the depth ratios should not be too small (indicating that all the inflection points have occurred at a similar depth) or too large (indicating a complex dive profile).

BSM point residuals (r1, r2, r3, r4): residuals obtained from fitting a linear regression model through the four BSM points. The residual of the start or end points of a drift segment should be expected to be negative for certain groups (indicated in Table 3).

mdepthbias: Difference between the time at maximum depth (T1) and half of the total dive duration. This should be positive for negative drift dives as the maximum dive depth occurs at the end of the drift segment, in the second half of the dive; and conversely negative for positive drift dives as the maximum dive depth should occur at the start of the drift segment, in the first half of the dive.

mdepthr: Ratio between the averaged depth of the BSM points and the maximum depth. Values close to 1 would be indicating small changes in depth along the dive, not to be expected in drift dives. Large values would indicate 'V' shaped dives.

BSM segment lengths (hp1, hp2, hp3): Euclidean length of the three dive segments, determined by the 4 BSM points. For two segments with the same duration, the segment with a larger change in depth will have a larger value.

Proportional duration of the BSM diving segments (ps1, ps2, ps3): proportion of the dive duration spent in the three segments defined by the BSM points. For a given drift segment, it should be reasonably large

Avratio: Deviation of the time at which maximum depth occurs, with respect to half of the dive duration (i.e., the midpoint of the dive). It is useful to determine the drift segment in some cases.

Occurrence of the inflection point with respect to the dive duration (t1, t2, t3, t4): i.e., t1 = T1 / Dive duration, t2 = T2 / Dive duration and so on. Here T1 refers to the time (in seconds) since the start of the dive at which the first inflection point occurred, and so on.

Mrratio: ratio between the length of the fourth (last) residual of the BSM and the maximum dive depth.

2.8.2 *Application*

All criteria are simultaneously compared between drift and non-drift dives for each of the 15 subgroups (8 negative and 7 positive). We constructed density plots of the dive variables with the overlapping area between drift (blue line) and non-drift (red line) dives shaded in dark (Figure A2.1). We made plots for each seal and for the three seals altogether to maximize removal of non-drift dives while minimizing removal of drift dives, thereby balancing the optimum threshold among the three seals.

Using these plots, the criterion showing less overlap between the density distribution of drift and non-drift dives was chosen and investigated in detail to choose the numerical threshold to maximize the rejection of non-drift dives while minimizing the rejection of true drift dives (Figure A2.2). For that purpose, the values considered reasonable were a reduction of around 50% (at least) of non-drift dives at the cost of up to around a 5% of the drift dives.

This procedure follows sequentially through the relevant criteria, we show two more examples below: for criteria ps1 (Figure A2.3 and 2.4) and t1 (Figure A2.5 and 2.6). The final number and percentages of retained certain drift dives across the eight major groups of candidate drift dives are given in Appendix B.

Figure A2.1. First example showing the application of the dive criteria and choice of threshold. Here, for negative drift dives of the group defined by the ifp 2.1.4.3. Once all density plots are visualized, the criteria showing less overlap between drift (blue)/non-drift (red) dives is chosen: d1 in this example.

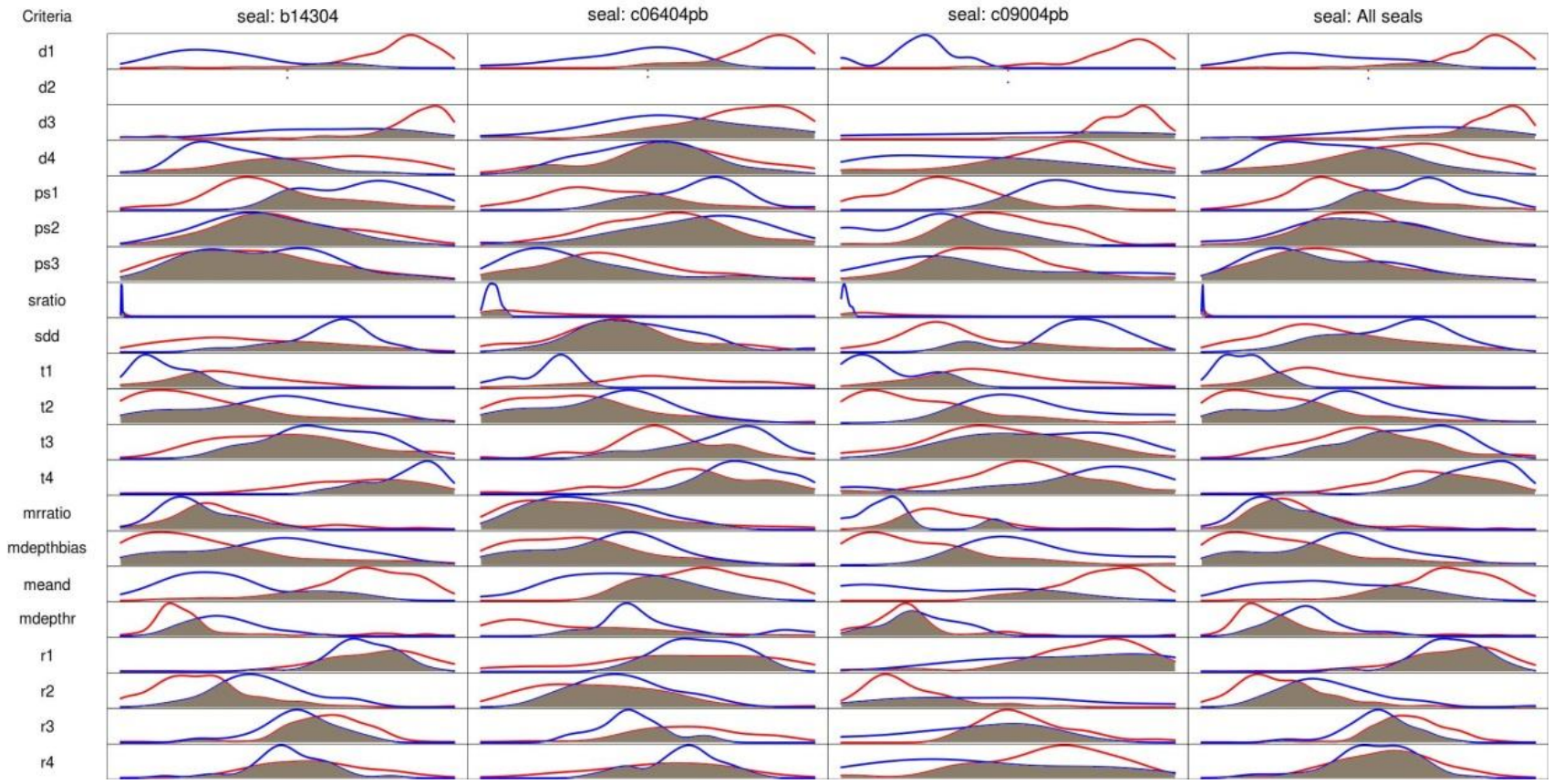


Figure A2.2. A reject-accept plot generated following the choice of criteria (here d1, from Figure A2.1). This shows the proportion of accepted drift and non-drift dives along a gradient in the threshold values is generated with the three seals, both independently and pooled.

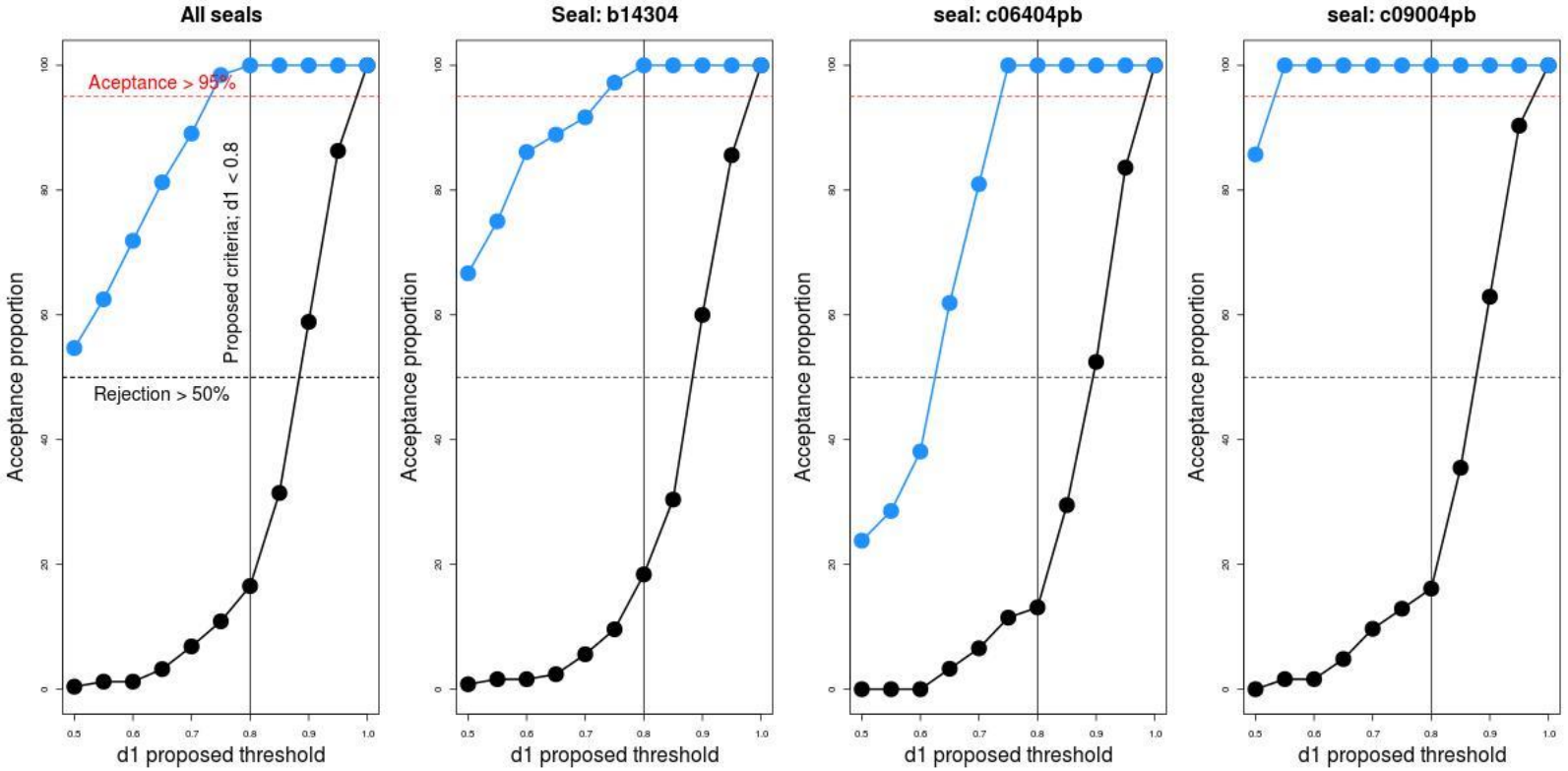


Figure A2.3. Second example showing the application of the dive criteria and choice of threshold. Following the choice of d1 above, ps1 in this example. Note that while previous criteria (d1) could have been optimized more for seals b14304 and c09004pb, it would have had a large negative impact on seal c064404pb. Blue is the density line of drift dives, and red of non-drift dives.

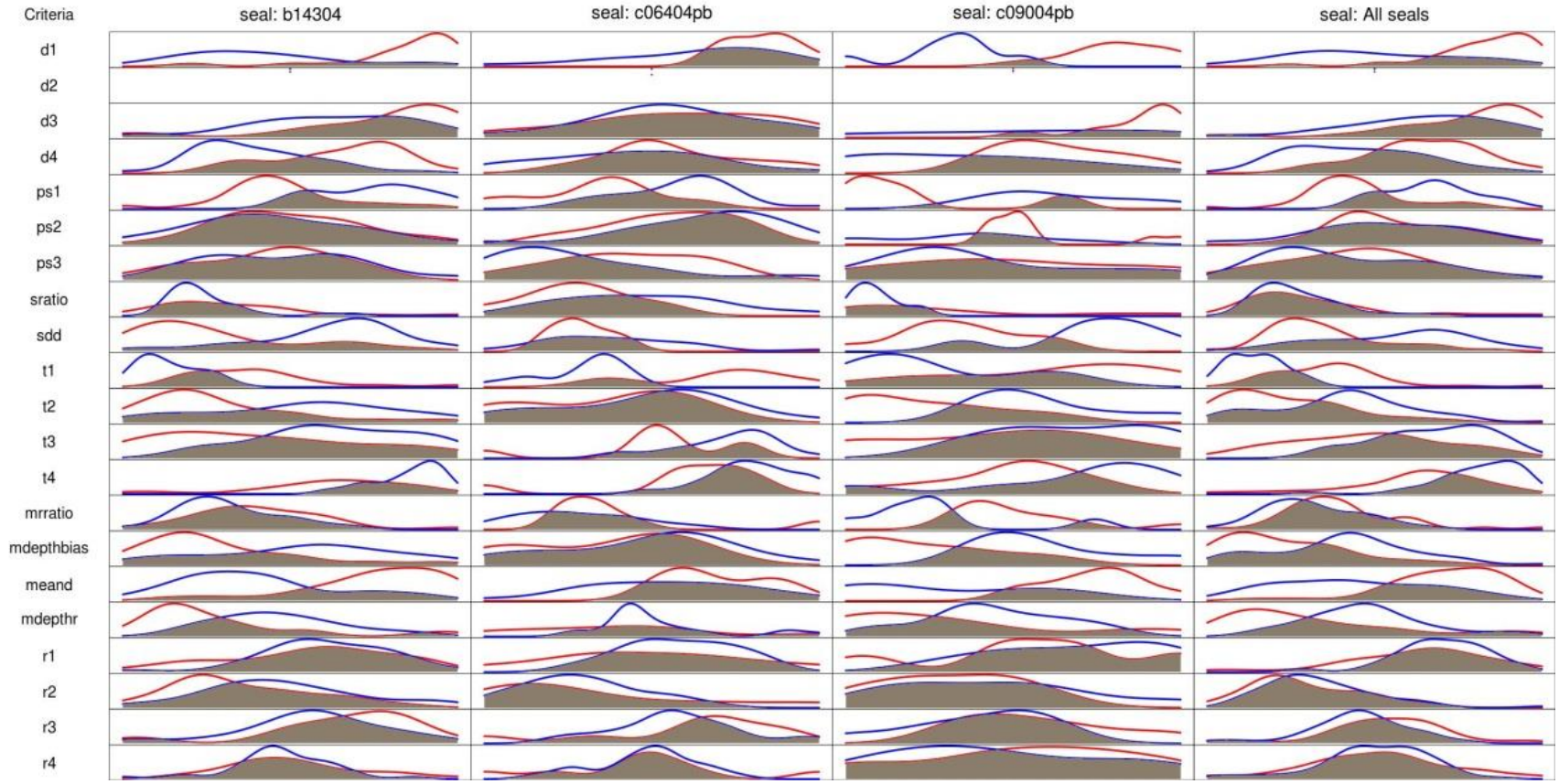


Figure A2.4. A reject-accept plot generated following the choice of criteria (here ps1, from Figure A2.3).

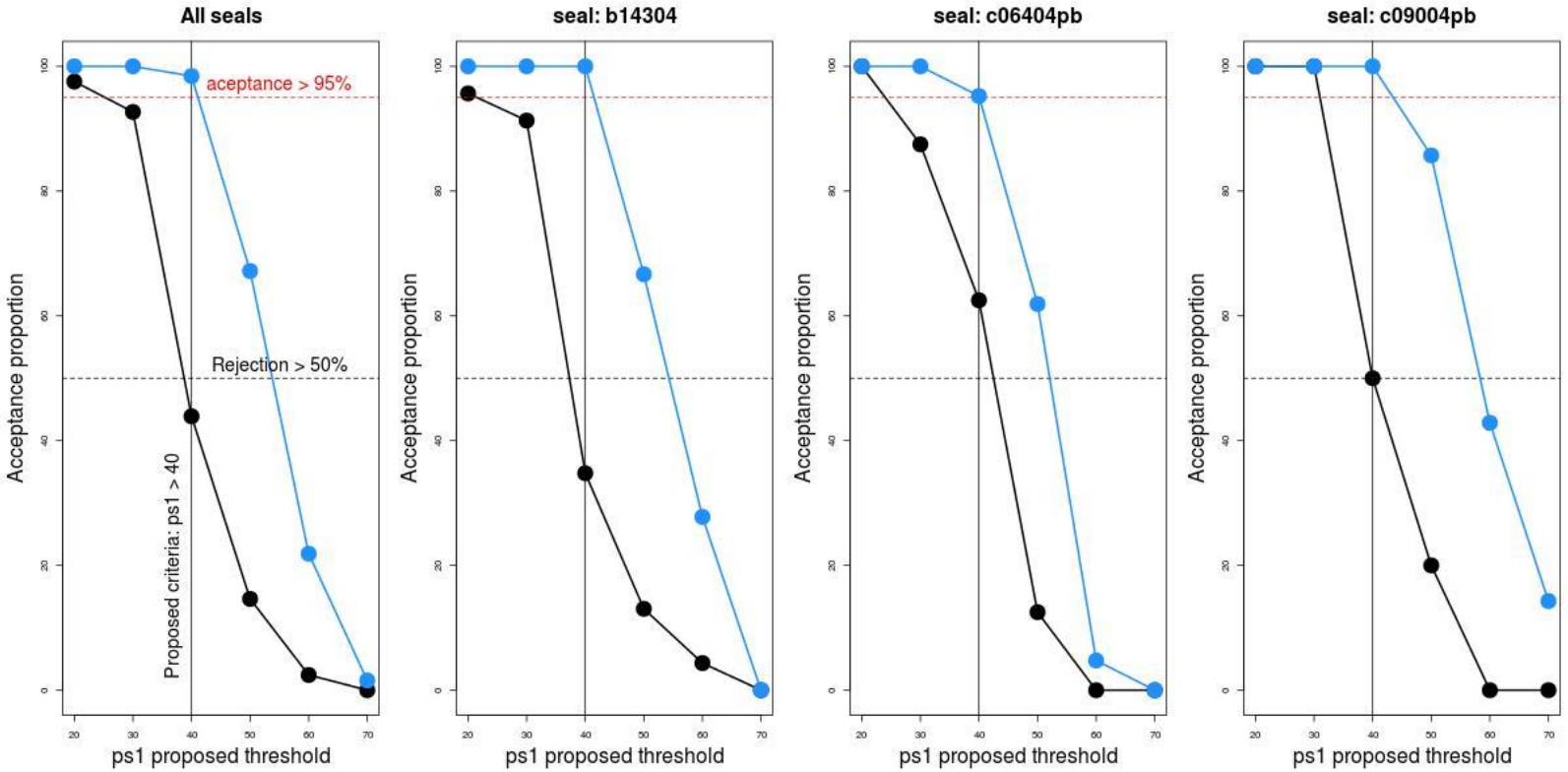


Figure A2.5. Third example showing the application of the dive criteria and choice of threshold. Following the choice of d1 and ps1 above, t1 in this case. Blue is the density line of drift dives, and red of non-drift dives.

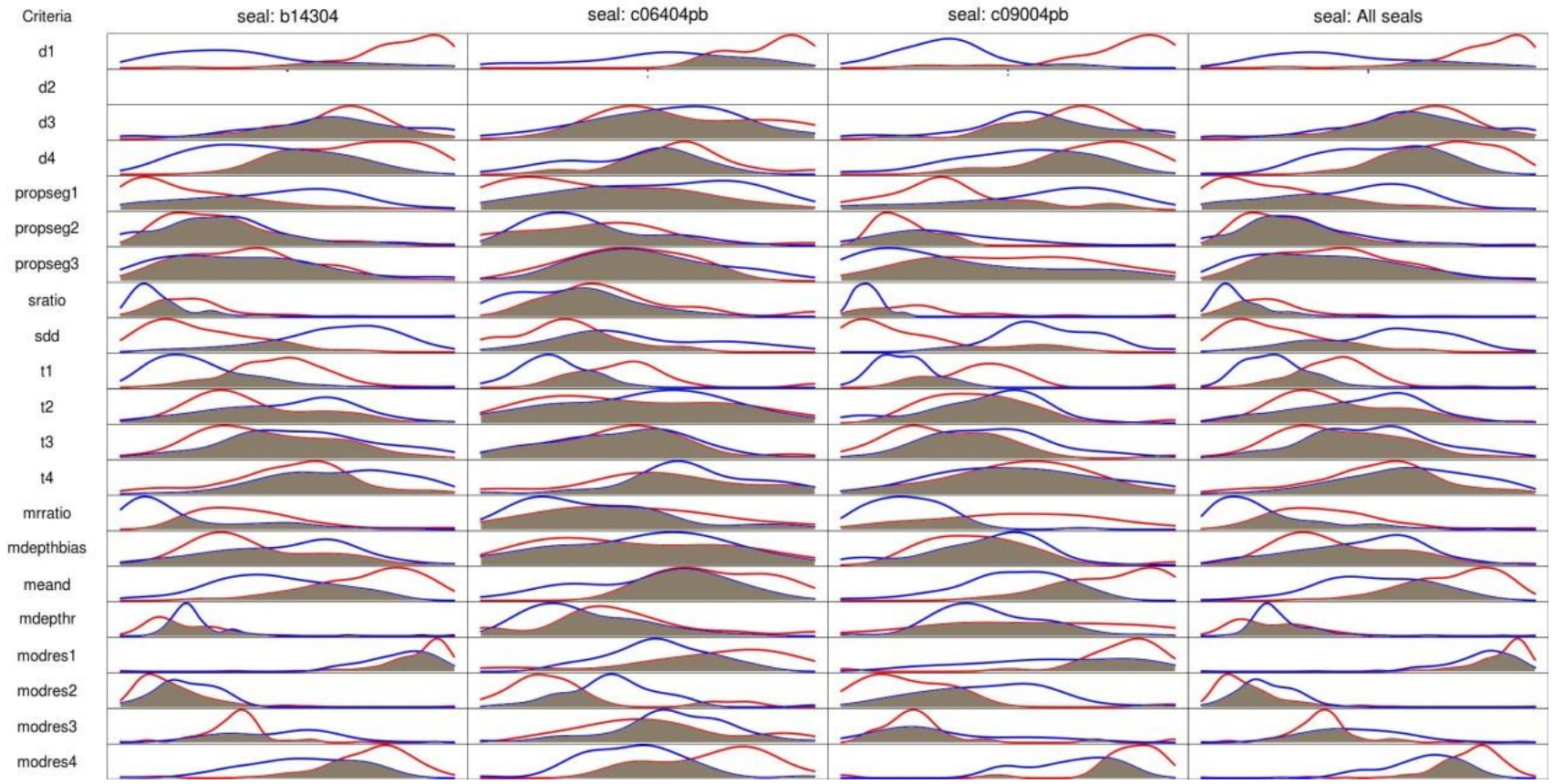
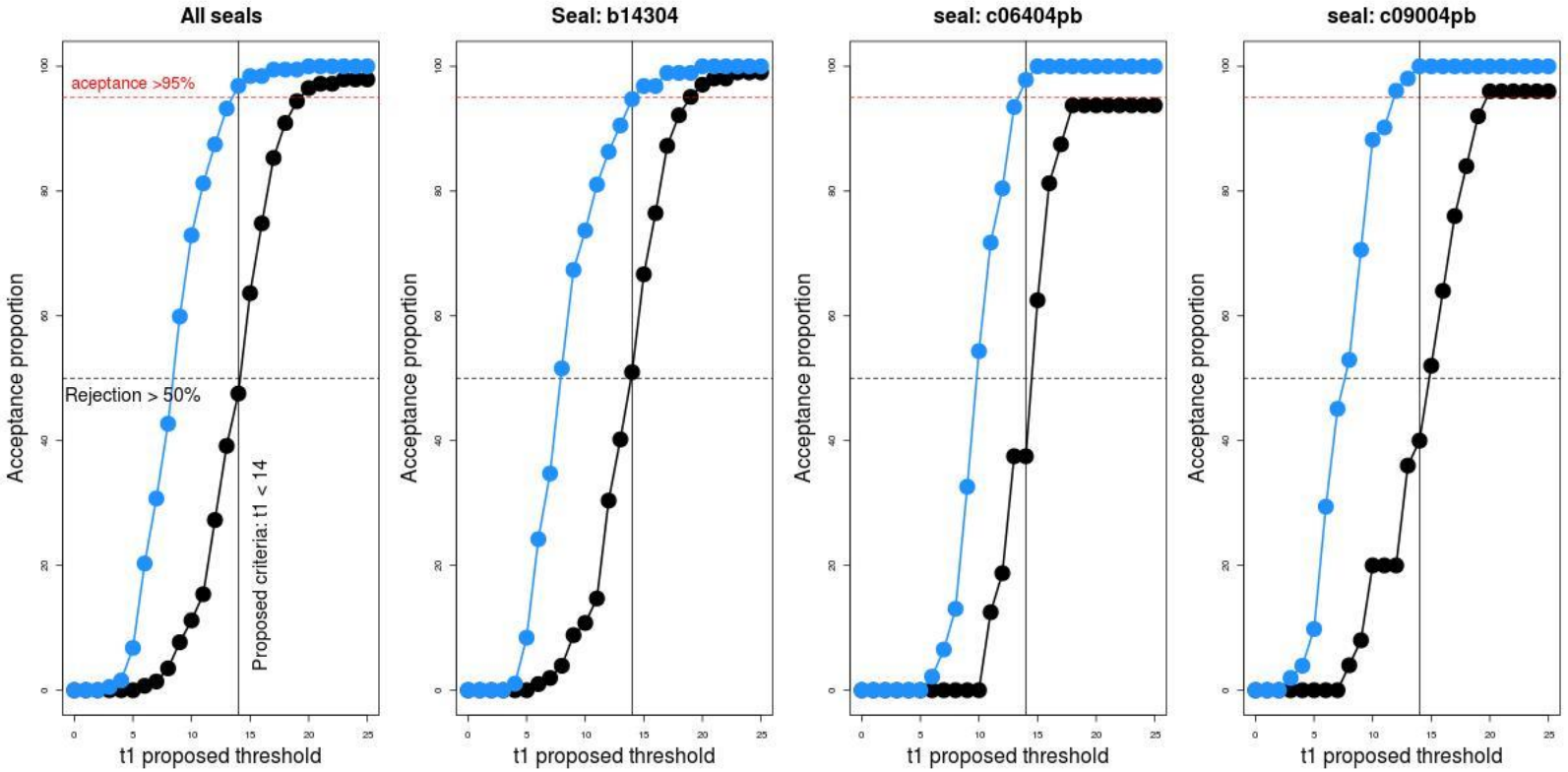


Figure A2.6. A reject-accept plot generated following the choice of criteria (here t1, from Figure A2.5).



2.9 Appendix B. Visual dive classification results.

Visual dive classification results for each visually inspected seal associated with each inflection point order generated with the reverse broken stick algorithm (RBSA). Dive types: 1 – not a drift dive, 2 – certain negative drift dive, 3 – uncertain negative drift dive, 4 – certain positive drift dive, 5 – uncertain positive drift dive. The eight major groups retained for generating the set of candidate drift dives appear in bold, with the number and percentages for the retained certain drift dives occurring within these groups also given below.

Seal Id →	b14304pm					c06404pb					c09004pb				
Dive Type →	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
RBSM group ↓															
1.2.3.4	8					2					2				
1.2.4.3	10					2	2				1				
1.3.2.4	49	1		2		8					8				
1.3.4.2	418			2	1	75					41				
1.4.2.3	83				1	30					24				
1.4.3.2	149				1	24					10				
2.1.3.4	**270**	**36**	7	**6**	**17**	**98**	7				**94**	**21**	**4**		
2.1.4.3	**864**	**110**	**8**	**4**	**6**	**183**	**53**	**1**			**175**	**48**	**2**		
2.3.1.4	196	3	1	1	1	63	2				20				
2.3.4.1	163	3	4			22					14	2			

2.4.1.3	**1775**	**27**	**4**	**7**	**7**	**653**	**8**	**2**			**488**	**6**	**2**		
2.4.3.1	509	4	5			70	1				66		1		
3.1.2.4	**562**	**9**	**1**	**85**	**9**	**372**	**16**	**2**			**378**	**22**	**4**		**6**
3.1.4.2	**2589**	**73**	**14**	**34**	**15**	**916**	**16**				**619**	**14**	**6**		
3.2.1.4	**109**	**86**	**5**			**27**	**23**				**19**	**9**	**1**		
3.2.4.1	214	9	5			62	11				29	2	1		
3.4.1.2	**608**	**4**	**1**	**11**	**4**	**311**	**6**				**149**	**2**	**2**		
3.4.2.1	29	3	1			2	2				4				
4.1.2.3	77	2	1	9		30					32				
4.1.3.2	258	21	3	2	3	62	1				35				
4.2.1.3	**676**	**141**	**26**	**7**	**5**	**399**	**36**	**1**		**1**	**261**	**64**	**9**		
4.2.3.1	105	2	2	1	1	22	1				15	1			
4.3.1.2	285	8		8	3	245	6				105	8	3		
4.3.2.1	24					3						1			
Total	10030	542	88	179	74	3681	191	6	0	1	2589	200	35	0	6
Retained		486		154			181					186			
Percentage (%)		90		86			95					93			

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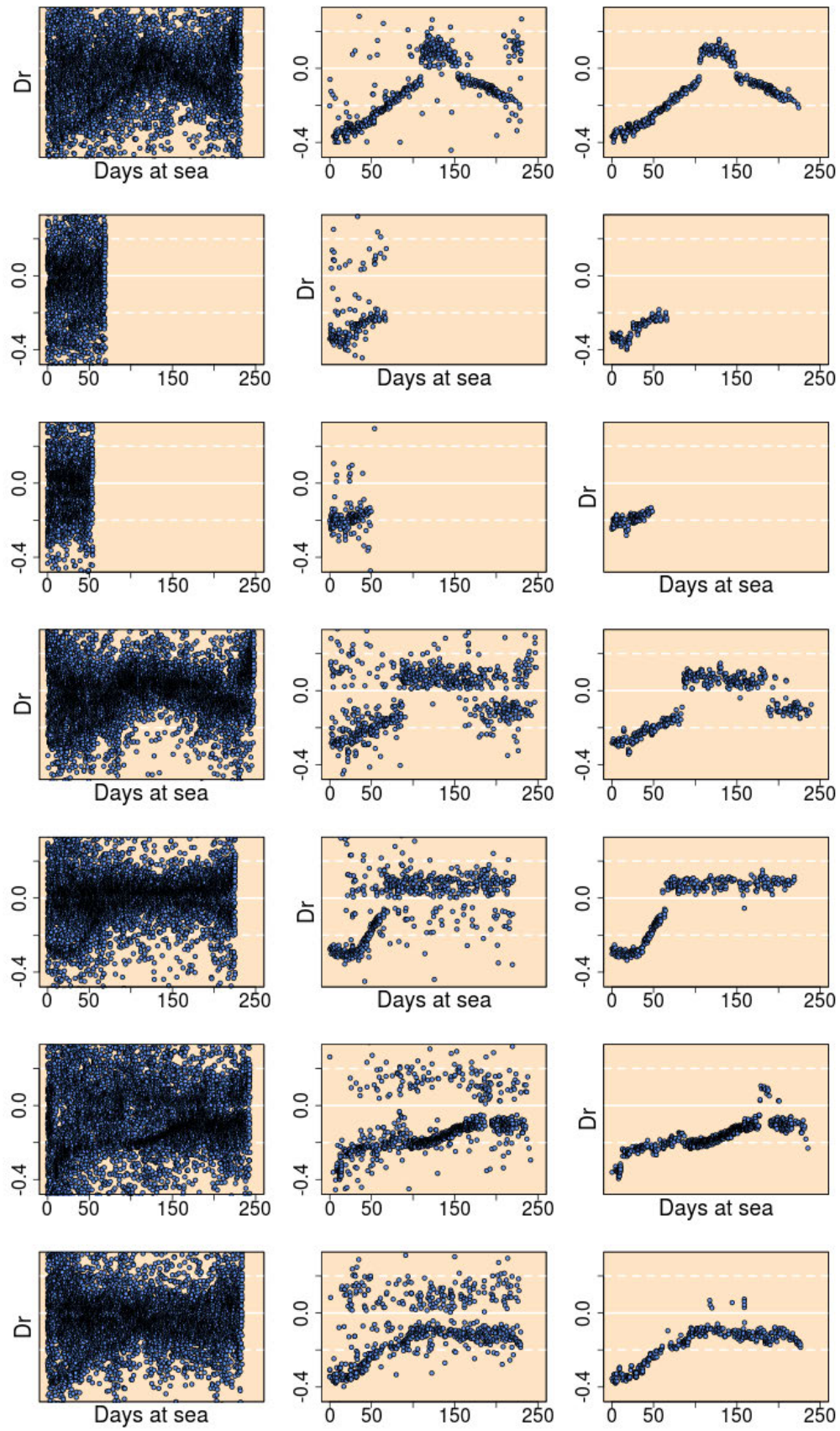
2.10 Appendix C. Visual representation of the complete filtering process.

Each seal (n = 13) is in a row, with seals used for developing the method occupying the first three rows. First column: the subset of candidate Drift dives based on the RBSA. At this stage, the drift segment is identified and drift rate calculated. Second column: dives remaining after the threshold criteria are applied across groups. Third column: final output after the Kalman filter where x-axis represents days at sea and y-axis represents drift rate. The numbers and proportions of dives retained at each step for the validation seals are available at Table 4 on the manuscript.



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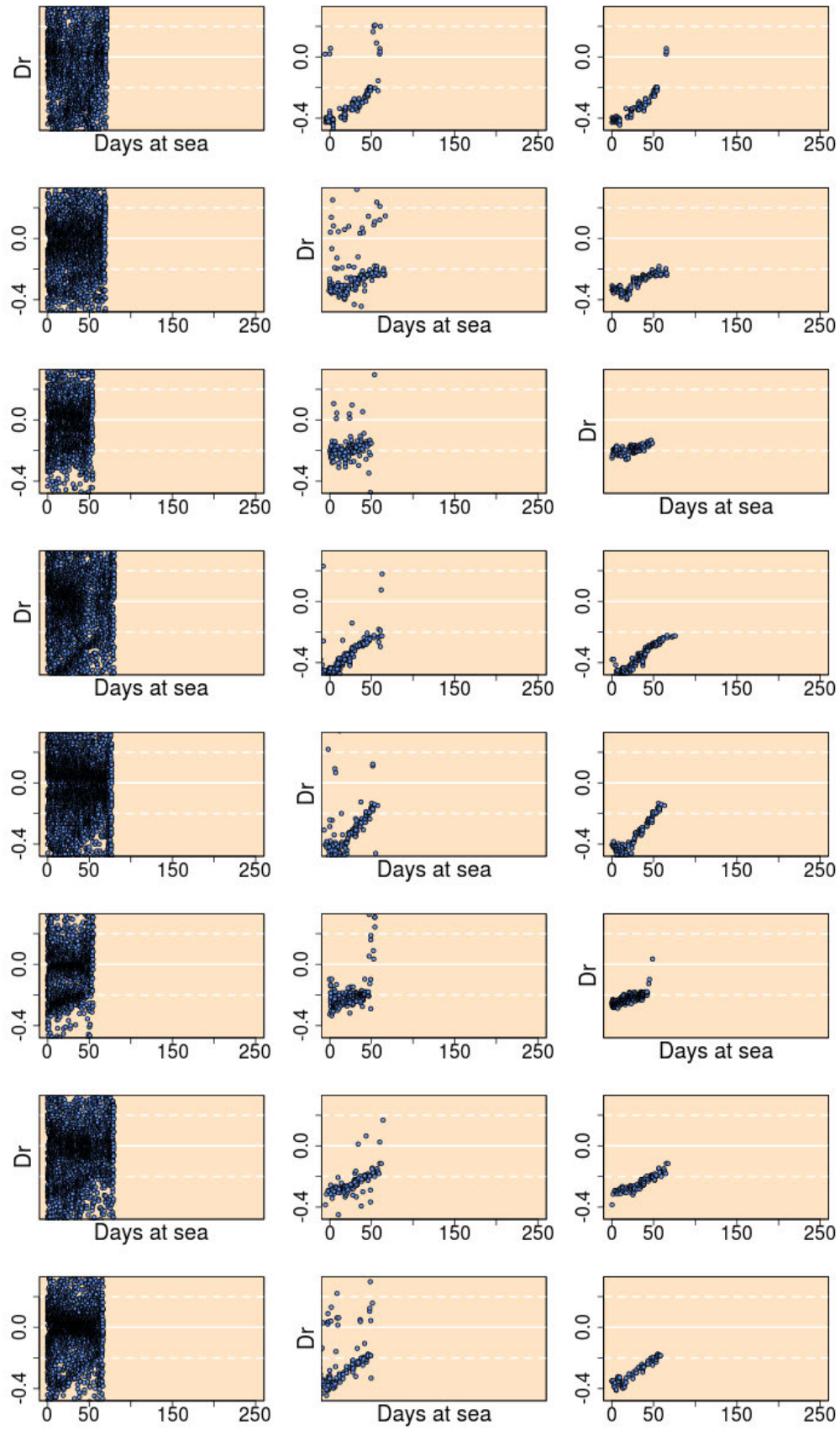
Dr
Days at sea
0.0
-0.4
0
50
150
250

Chapter 3 *SlimmingDive*: Flexible, Hierarchical Selection of Drift Dives

https://github.com/farcego/slimmingDive

Scientific research is increasingly dependent on large, complex analyses. This has led to a growing interest in implementing practices of reproducible research in the academic world, as has been known for a long time in the computer science community (Wilson et al., 2014). In parallel, researchers are now more frequently exposed to command-line interfaces and programming languages, allowing them to use and develop domain-specific analyses, often not available in general-purpose analytical software. Alas, most researchers have not received formal training in programming even if they spend a substantial part of their research time programming (Hannay et al., 2009). Thus, good practices for reproducible research have been promoted over recent years in the form of journal articles (Wilson et al., 2014, 2017), and also via academic workshops (notably, via the Software Carpentry developed workshops for the academic community: https://software-carpentry.org/) and MOOCs (massive online open courses). Several software platforms have already developed process and routines to stimulate literate programming, a recommended practice to enhance reproducibility, and most scientific journals have started to implement mechanisms in their policies to improve the reproducibility of the research they publish (Nosek et al., 2015). These policies may vary among journals but typically include enforcing authors to make the data used in their articles publicly available, and/or require code sharing for novel or non-standard methodological approaches (see for example, the editorial policies of the British Ecological Society: https://besjournals.onlinelibrary.wiley.com/hub/editorial-policies). They also support the use of free, open software (Nosek et al., 2015; Tippmann, 2015; Wilson et al., 2014, 2017).

In this context, while there are a number of general purpose free software tools for data analysis, R statistical language (R Core Team, 2018) has become one of the most commonly used programming tools in the academic world. It can have a steep learning curve, but the implemented analytical tools make ita general tool of choice in ecological research. One of the biggest strengths of R is that is easily expanded through contributed packages (Marwick, Boettiger, & Mullen, 2018), some of them designed to interact with other programming

languajeslanguages like c++, Python, or jags. R packages are structured pieces of code that expand the R base functionality. They may be developed to enhance currently implemented functionality, or to implement domain-specific analytical tools. Currently, there are ~15,000 packages hosted on CRAN (the Comprehensive R Archive Network, see https://cran.r-project.org/web/packages/), plus a probably equivalent number released in other platforms or developed for private use.

While releasing R source scripts would be sufficient for the current standards of the academic world, in term of enabling reproducibility, here we provide the research community with an R package. The minor disadvantages associated with creating an R package (e.g. often time consuming to generate documentation, description files and compliance with R build standards) are well compensated by its advantages, especially from the point of view of a potential end user. First, the code released in the form of a package is easy to install and to load. A package provides structured help files for each function, making it easier to use. They often include a vignette, with a guided example and case data. Besides, the source code is always available and can be inspected at any time. R packages work better when it comes time to improve/update the code. As packages are also easier to update and install, the end-user will have an updated version at any time, without having to deal with multiple source files/versions.

slimmingDive is thus implemented in R. It has been designed to make it easier for researchers to follow the methodology developed to detect drift dives and estimate drift rates for elephant seals (Arce, Bestley, Hindell, McMahon, & Wotherspoon, 2019a). Besides R, the main dependency is JAGS -Just Another Gibbs Sampler- (Plummer, 2003), for the Kalman filter implementation. ***Slimmingdive*** uses the R package *rjags*, to interface with JAGS. ***slimmingDive*** is operating system *agnostic*. It has been developed on a GNU Linux environment, and has been tested to work under Windows and macOS environments.

3.1 Installation

We recommend users install JAGS and *rjags* prior to ***slimmingDive***. It should work with relatively recent versions (R ≥ 3.5.1 and jags ≥ 4.2.0). ***slimmingDive*** is currently available only

at GitHub, and is perpetually archived in Zenodo ((Arce et al. 2019a). To be installed, the recommend approach is to use *remotes* package:

```
remotes::install_github('farcego/slimmingDive')
```

and to load the package:

```
library(slimmingDive)
```

3.2 Data requirements

The package has been developed bearing in mind the data format delivered directly from SMRU (Sea Mammal Research Unit) Satellite Relay data loggers tags. Thus, the data are expected to have been pre-processed onboard the tag with a broken-stick algorithm (Fedak et al. 2002). The variables needed and their exact name and formats are provided below:

ref: unique identification code for the seal/tag

DE_DATE: date of a given dive. Needs to be in POSIXct format

D1: depth of the first inflection point (in meters)

D2: depth of the second inflection point (in meters)

D3: depth of the third inflection point (in meters)

D4: depth of the fourth inflection point (in meters)

T1: time of the first inflection point, proportional to the dive duration

T2: time of the second inflection point, proportional to the dive duration

T3: time of the third inflection point, proportional to the dive duration

T4: time of the fourth inflection point, proportional to the dive duration

MAX.DEPTH: maximum depth of the dive (in meters)

DIVE_DUR: dive duration (in seconds)

3.2 Example of use

3.2.1 Example data-set

```
data(ele) # load the example seal provided with the package
dim(ele) # check the data
    # [1] 6584   48
```

The example dataset contains 6584 dives, and 48 columns. Most of the columns of the data.frame are of no interest for drift dive selection purposes, and some lack the appropriate format). Function *formatDives* will handle this, by removing the unwanted columns, change DE_DATE format, re-name some columns and filtering a small subset of dives of no interest for drift dive selection purposes (dives shallower than 100 m and shorter than 300 sec).

```
ele <- formatDives(ele)
```

The following procedures can be classified into two steps: variable generation, then dive filtering.

3.2.2 Dive variables generation

The variables first required are the order of the inflection points, generated by applying a reverse Broken-stick algorithm ((Photopoulou et al. 2015b), and the size (m) of the last residual (as an indicator of the remaining variance in vertical movement not well captured by the dive summarization).

```
ele[c('order','minresid')] <-
        t(apply(ele,1,RBSM,retrieve='both'))
ele$minresid <- as.numeric(ele$minresid)
```

Now, we can compute the new variables needed to undertake the first step of the filtering process:

```
ele <- NewVarsVect(ele)
```

Finally, these variables are used to define the drifting segment and its associated drift rate:

```
ele [c('NDE','ds')] <- t(apply(ele,1,NDE, extract='both'))
```

At this point, we have actually calculated a drift rate value for each of the dives. As the dataset has not yet been filtered, visualization at this point shows the drifting trajectory is not easy to pick up due to the noise added by all non-drift dives (Figure 1). It can now be visualized using a custom plotting function from ***slimmingDive*** called *plotDrift*:

```
plotDrift(ele, xlab = 'foraging days', ylab = 'Drift rate',
          xlim = c(-10, 245))
```

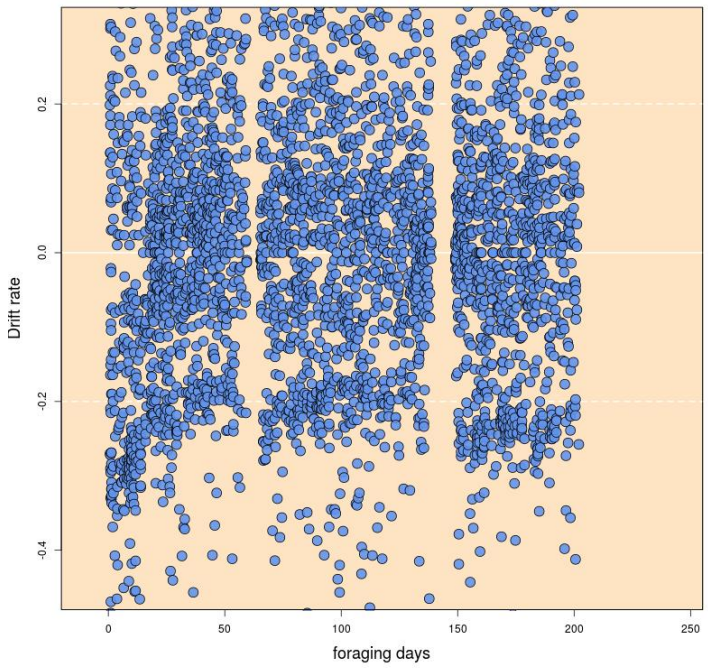

Figure 3.7. ***Graphical representation of the drift rate (cm s^{-1}) from the complete dive dataset (including all potential drift dives).*** *At this stage, only a basic filtering process has been imposed (dives shallower than 100 m and shorter than 300 sec) to the dataset, thus the information is not yet useful. Interestingly, this seal seems to have performed two haul-outs (periods on land).*

3.2.3 Filtering process

Once we apply the filtering process via the *driftFilter* function, the drifting trajectory remains still a bit noisy, but now quite apparent (Figure 2).

```
ele <- driftFilter(ele)
```

```
plotDrift(ele, xlab = 'foraging days', ylab = 'Drift rate',
          xlim = c(-10, 245))
```

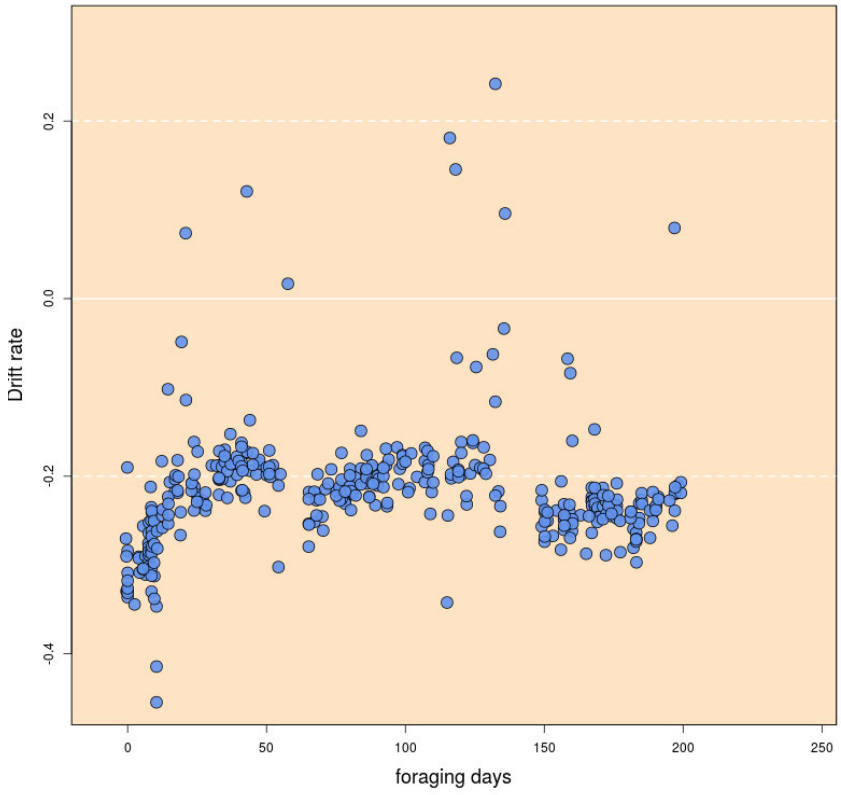

Figure 3.8. ***Drift rate trajectory after applying the first filter (via the* driftFilter *function).*** *The drifting trajectory is revealed, but still remains quite noisy and requires some extra processing.*

To remove the unrealistic values from the drift trajectory time series, we use the last step of our filtering process and run a custom Kalman filter to remove erroneous locations inconsistent with the drifting trajectory:

```
ele<- Kalman(ele,400000, 10000)
```

The example dataset can require 10-20 min to be processed (the final time depends on both the number of candidate drift dives and the CPU speed). The *Kalman* function generates a large amount of information regarding the model that is of relatively little importance to the average user; we can post-process it with the *PostKalman* function:

```
ele<- PostKalman(ele)
```

And finally, we keep only those dives with a high probability of being drift dives (in this example, we set the probability threshold at 95%).

```
ele<- ele[ele$zetas > .95, ]
```

finally, we can see the seal drifting trajectory again with *plotDrift* function:

```
plotDrift(ele, xlab = 'foraging days', ylab = 'Drift rate',
                    xlim = c(-10, 245))
```

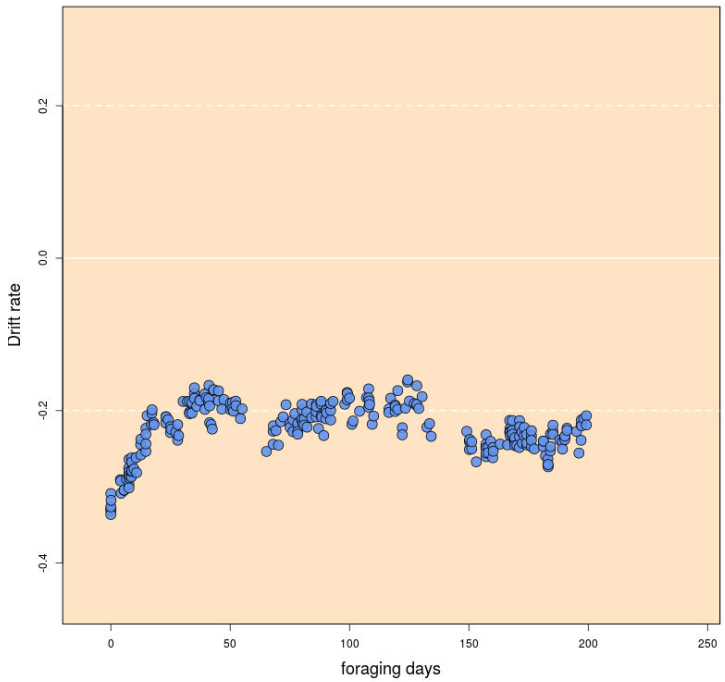

Figure 3.9. ***Final drifting trajectory after applying the Kalman filter.*** *The pattern obtained matches with the expectation of a catastrophic moulter. It shows the lowest body condition at the start of the foraging trip, followed by a gradual increase. As expected, after the two haul-outs (periods during which the elephant seals fast on land) the seal has lost body condition and is less buoyant than at the start of the haul-out periods.*

3.3 Availability

slimmingDive package is currently available at GitHub, and archived in a zenodo repository:

https://github.com/farcego/slimmingDive

https://zenodo.org/record/3255153#.XW9LKigzZaQ

3.4 Future versions/releases:

- Implement a custom link for the R *gam* (generalised additive model) function to unconstrain the estimation of the drift rate at any particular time-scale. This has been implemented and will be available in the next release.

- Implement a parallelised version of the Kalman filter to reduce computation time. It has been developed under the Linux environment, but pending testing for Windows or macOS environments.

- Planning: test the usability of the Kalman filter to improve the methods developed to detect drift dives from high-resolution (unsummarized) dive information.

Chapter 4 Enhanced foraging success of an Antarctic top predator within Antarctic coastal polynyas

4.1 Introduction

Polynyas are recurrent areas of open water or fragmented thin-ice surrounded by sea ice (Morales Maqueda et al. 2004). Around Antarctica, coastal polynyas are generally maintained by katabatic winds advecting sea ice away (Arrigo and Van Dijken 2003), and when active they sustain high ice production rates. While Antarctic shelf polynyas may be covered by thin ice during the winter they are the first areas where sea ice melts, enabling earlier phytoplankton growth and enhancing the energy flux though to mid- and higher-trophic levels (Arrigo and Van Dijken 2003, Arrigo et al. 2015). Through increased vertical carbon flux polynyas may also support rich benthic communities (Grebmeier and Barry 2007, Jansen et al. 2018). The benefits of high primary productivity, boosted by iron supply from basal melting of coastal glaciers, remain through the summer season and later on (Arrigo et al. 2015). During late summer and in the inactive periods, polynya locations and their impacted surroundings can therefore be considered as "post-polynya" areas (Arrigo and Van Dijken 2003, Raymond et al. 2015, Arrigo et al. 2015, Bestley et al. 2018). This makes polynyas important sites of biological production which can attract organisms from all trophic levels, forming rich ecosystem aggregations from phytoplankton to top predators.

Polynyas are widely known to be used year-round by marine mammals and seabirds (Stirling 1980, 1997, Karnovsky et al. 2007, Raymond et al. 2015) including whales (Thiele and Gill 2007), penguins(Ancel et al. 1992) and seals (McMahon et al. 2002, Heerah et al. 2013). However, the ecological benefit of polynyas for particular species has rarely been directly quantified. One recent example demonstrated a positive relationship between annual primary production in two Antarctic polynyas and pup production by ice-dependent Weddell seals (Paterson et al. 2015).

Southern elephant seals are marine predators that breed in the sub-Antarctic region, often foraging over the Antarctic continental shelf and in surrounding waters (Hindell et al. 2016). As capital breeders with a catastrophic moult, individual seals must fast on land for several weeks

during the two energetically demanding breeding and moult periods; the energy for these fasts must be acquired at sea beforehand (Laws 1953, Fedak et al. 1994). They exhibit a dramatic sexual dimorphism and an extreme polygynous breeding system (McCann 1981, Galimberti et al. 2002, Fabiani et al. 2004). Recent work in the Indian sector of the Southern Ocean has pointed out that immature southern elephant seal males from the Kerguelen Island population visit East Antarctic coastal polynyas through summer, and often concentratethere through winter (Malpress et al. 2017, Labrousse et al. 2018). They were found to modify their diving patterns and their movement behaviour inside the polynya zones (Labrousse et al. 2018). Little is known about the degree to which females use these regions as they tend to concentrate foraging in areas of deep water, rather than shelf areas (Hindell et al. 2016).

In this study I aim to determine whether post-polynya areas provide better foraging conditions than surrounding Antarctic waters. If polynyas are better foraging grounds, one should expect enhanced individual foraging success while inside. Here, we address two questions: (i) which elephant seals use polynyas? (ii) How large is the benefit to the seals using polynyas? Polynya usage is examined with respect to movement behaviour, sex and deploymentlocation. Behavioural changes are determined from movement data using state-space models (Jonsen et al. 2003, 2013, 2019, Patterson et al. 2008) to identify 'in-transit' vs 'area restricted search' locations. In elephant seals, foraging success can be quantified using changes in drift rate between consecutive positions. During drift dives seals are passive in the water column (Crocker et al. 1997) so the rate of change in depth is directly linked to the seal's buoyancy, mostly determined by the fat:lean tissue ratio (Biuw et al. 2003). Drift rate therefore enables *in situ* changes in body condition to be monitored at sea (Biuw et al. 2003, 2007, Bailleul et al. 2007b, Gordine et al. 2015, Arce et al. 2019b).

4.2 Material and methods

4.2.1 Seal tagging data

More than two hundred southern elephant seals have been instrumented in the Indian Ocean under the Australian Integrated Marine Observing System program (IMOS 2019) over the last decade (Supplementary material, table S1) with Conductivity Temperature Depth - Satellite Relay Data Loggers (CTD-SRDLs, Sea mammal research unit, University of St. Andrews, UK). Adult females and immature males were tagged on Kerguelen Island (n=112), the main breeding

colony of the Southern Indian Ocean, and at two moulting sites in East Antarctica, Prydz (n=48, only immature males) and Vincennes Bay, (n=24, immature males plus 2 adult females) (Van Den Hoff et al. 2003). See supplementary information Table 1 for detailed information of tagging numbers by year, location, and sex. Capture and sedating procedures have been fully described elsewhere (McMahon et al. 2000a, Field et al. 2002). CTD-SRDLs record depth (Fedak et al. 2002, Photopoulou et al. 2015a) data summarized by a broken-stick algorithm (Fedak et al. 2002, Photopoulou et al. 2015a) and transmitted though the Argos satellite system (Argos 2011). Every time the instrument uplinks information via ARGOS, the location of the seal is determined by the Doppler effect (Argos 2011). Due to transmission constraints, the final diving dataset for each seal represents a random subsample of all dives comprising around 80% of the dives(Fedak et al. 2001, 2002, Boehme et al. 2009). We processed tracks using a hierarchical state-space model (Jonsen et al. 2013, Jonsen 2016) to account for ARGOS location error and reconstruct a 6-hour regularized path, and as well as provide an estimate of the horizontal behaviour (in-transit vs area-restricted search). The hierarchical state-space model was implemented using the R package *bsam* (Jonsen et al. 2005) in R version 3.5.2 (R Core Team 2018), with tracks processed in batches defined by deployment year/location.

4.2.2 Estimating changes in body condition of SES

Drift dives are characterized by a long, inactive (non-swimming) phase during which the seal passively drifts in the water column (Webb et al. 1998, Biuw et al. 2003), during which the rate (cms^{-1}) and direction of the vertical displacement depends largely on the seals body condition. With the buoyancy of elephant seals being primarily determined by the ratio of lean tissue: blubber (Biuw et al. 2003), negatively buoyant seals will passively descend in the water column, while positively buoyant seals will passively ascend. We processed the summarized CTD-SRDL dive information following the methodology described in Arce et al. (2019a), keeping all dives with a high probability of being drift dives (Z > 0.5, See s2.3.3 Chapter 3). To assign an average drift rate to each 6 h location estimate, we fitted to each seal a generalized additive model (GAM) with a custom link function that takes into account the buoyancy model implemented in R package slimmingDive (Arce et al. 2019a).

4.2.3 Definition of temporal coverage, geographical study region, and Antarctic foragers

We focus on the first part of the seals' lengthy post-moult trips during the austral winter (first 180 days at sea). After moult seals have low body condition that must be recovered (Hindell et al. 1994); hence, the speed of fat reserve recovery is most pronounced during the early phase of the trip and tends to stabilize in the following months (Arce et al. 2019b). That rate of energy gain is directly determined by foraging success. Additionally, this occurs during the summer period (December-April), when large areas of the Antarctic shelf are ice-free and available to foraging seals (Arrigo et al. 2015). Therefore, during this time we can test behavioural and foraging differences between "post-polynya" areas and the rest of the Antarctic region. It potentially becomes more difficult to interpret whether seals would be favouring polynyas, or just being restricted by increasing ice concentration, as the winter season progresses and the sea ice advances. Focusing our approach on the first part of the seals' lengthy post-moult trips we restrict the modelling analyses to the first two months (60 days) foraging at sea, prior to the build-up of winter sea-ice.

The use of the Indian Ocean subsector by elephant seals can be broadly considered as either sub Antarctic or Antarctic(Hindell et al. 2016).

Idefined Antarctic foragers as those seals that spent at least 50% of the 60-day period south of 58.5°S (supplementary material figure s1), and removed the rest of the seals. Individuals with drift rate information for less than 10 days in total were also excluded as they did not provide drift rate change trajectories of sufficient length to provide a reliable estimate of change in condition. Table S1 provides a summary of the seal (n = 119 individuals) considered in this study.

Given that seals may moult and be tagged any time between late December and early March, Iset time zero (t_0) for each individual to be the time when they first exhibit drift diving behaviour, discarding the earlier part of the post-moult trip. Since drift dives are thought to be related to food processing (Crocker et al. 1997, Mitani et al. 2010, Watanabe et al. 2015), they may delay the start of foraging during the earlier part of the trip, on transit to the foraging grounds (Crocker et al. 1997). Icalculated the rate of change in the drift rate for each location (ΔDr_i) as the

difference between the drift rate values obtained from the gam smoothingat the current (Dr_i) and previous (Dr_{i-1}) locations, divided by the time increment between them (ΔT_i):

$$\Delta Dr_i = (Dr_i - Dr_{i-1})/\Delta T_i$$

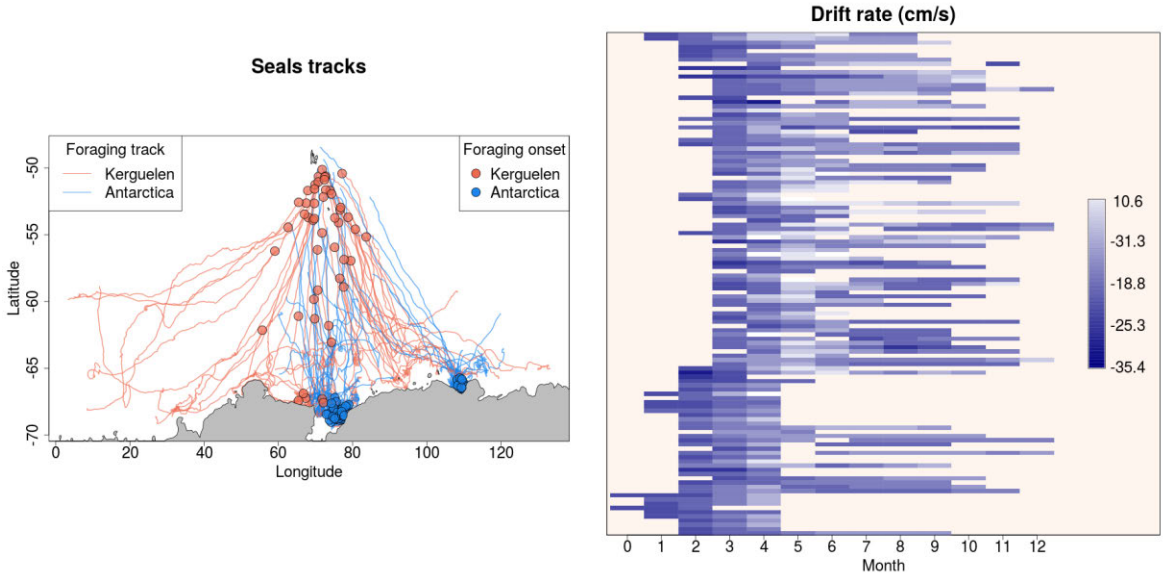

Figure 4.10. ***Foraging trips and body condition trends.*** *(A) Map showing filtered tracks of the post-moult foraging trips of 50 (69) seals tagged in Kerguelen (Antarctica). The commencement ofDrift diving behaviour is represented by a dot. (B) Heatmap showing elephant seal body condition through time, where darker blue indicates poorer condition. One seal is represented per row (n = 119). Horizontal axis shows month; here 1 to 12 is continuous, with month 12 referring to December for tags that transmitted throughout the year (i.e. cessation before moult). Month 0 is appended to represent December for those seals tagged in December (i.e. after moult).*

4.2.3 Modeling polynya usage and foraging success

I designate post-polynya areas according to Arrigo et al. (2003). I fitted generalized linear mixed models with the response variable being whether a location was inside or outside a polynya area, using a binomial distribution as appropriate for 0-1 data. Candidate predictors considered as fixed effects were the behavioural state estimate (1: in transit or 2: area restricted search), sex (male or female), tagging location (Kerguelen Is. or Antarctic coast) and ΔDr (i.e. the drift rate change). Seal identity was included as a random effect in all mixed models. We fitted the candidate models using R package *lme4*(Bates et al. 2015), assessing all combinations of fixed

effects using the R package *MuMIn*(Bartoń 2018) and comparing them using a second order AIC (Burnham and Anderson 2002).

I also examined the determinants of changes in drift rate by fitting linear mixed models using ΔDr rate as the response variable. Fixed effect predictors considered were polynya (inside/outside), tagging location (Kerguelen Is./Antarctic coast), behavioural state estimate (in transit/area restricted search) and sex (male/female). We incorporated a continuous time autocorrelation structure (corCAR1) since the values generated by the (smoothing) GAM function are not independent. We fitted candidate models with the R package *nlme* (Pinheiro et al. 2019) and compared them as above.

4.3 Results

Overall, 45% (n=50) of the seals instrumented at Kerguelen Is. spent at least half their tracked time within the Antarctic area, representing 50% (n=28) of tagged males and 33% (n=22) of tagged females (electronic supplementary material, table s1). The location of the first drift dive record, occurred either during transit or after arriving at the Antarctic shelf at an overall average distance of 837 km from the island (sd = 579, n = 50; figure 1A, electronic supplementary material, figure s2). 27 out of 28 (96%) of the Antarctic foraging males tagged at Kerguelen Is. spent at least some time inside coastal polynyas (median = 62%, range 3.4-100%, electronic supplementary material, figure s3). In comparison, only 4 out of 22 (18%) females from Kerguelen Is. that travelled to the Antarctic region visited polynyas, spending a variable proportion of their time here (0.4, 2.5, 27 and 40%; electronic supplementary material, figure s3). Of those seals instrumented in Antarctica, 96% remained as Antarctic foragers (electronic supplementary material, table s1), commencing foraging at an average distance of 67 km (sd = 48, n = 69) from the tagging location (figure 1A, electronic supplementary material, figure s1). All the males tagged in Antarctica (n = 67) spent at least some time inside polynyas (median = 64%, range = 1.4-100%). Only two females were tagged in Antarctica and both remained as Antarctic foragers but spent little time inside polynyas (1.6 and 36%).

4.3.1 Body condition at the commencement of drift diving

Elephant seals showed consistently low drift rates during the early part of their post-moult foraging trips (figure 1B). The mean overall drift rate at the start of the study period was -29 cm

s^{-1} (sd = 6 cm s^{-1}, n = 119). Males instrumentedat Kerguelen had a mean start value of -33 cm s^{-1} (sd = 6, n = 28), and the females -30 cm s^{-1} (sd = 5, n = 22).Males instrumented in Antarctica had a mean start value of -28 cm s^{-1} (sd = 5, n = 67), while the two females had start values of -14 and -26 cm s^{-1}.

4.3.2 Polynya usage

Seal movements exhibited a clear transiting behaviour between the breeding colony and the Antarctic shelf, both when outbound from Kerguelen Is. to the Antarctic shelf and when returning to Kerguelen Is. (figure 2). Once over the Antarctic shelf region, area restricted search behaviour was evident inside and immediately around the post-polynya regions (figure 2).

The best model for polynya usage retained sex, ΔDr, and behavioural state as predictors (table 1) with the two highest ranked models (with or without tagging location) essentially equivalent (i.e. ΔAIC<1, electronic supplemental material, table s2). Antarctic foraging males that were tagged at Kerguelen Is. or on the Antarctic continent were similarly likely to visit post-polynya areas, while females were much less prone to visit polynyas than males. Locations inside polynyas were associated with more area restricted search behaviour and with positive changes in drift rates (electronic supplementary material figure S2).

4.3.3 Changes in Drift rate

For seals that provided drift rate information throughout the full study period (n = 90), the mean drift rate after 60 foraging days was -11 cm s^{-1} (sd = 13) with an average increase of 0.31 cm d^{-1} (sd = 0.21)

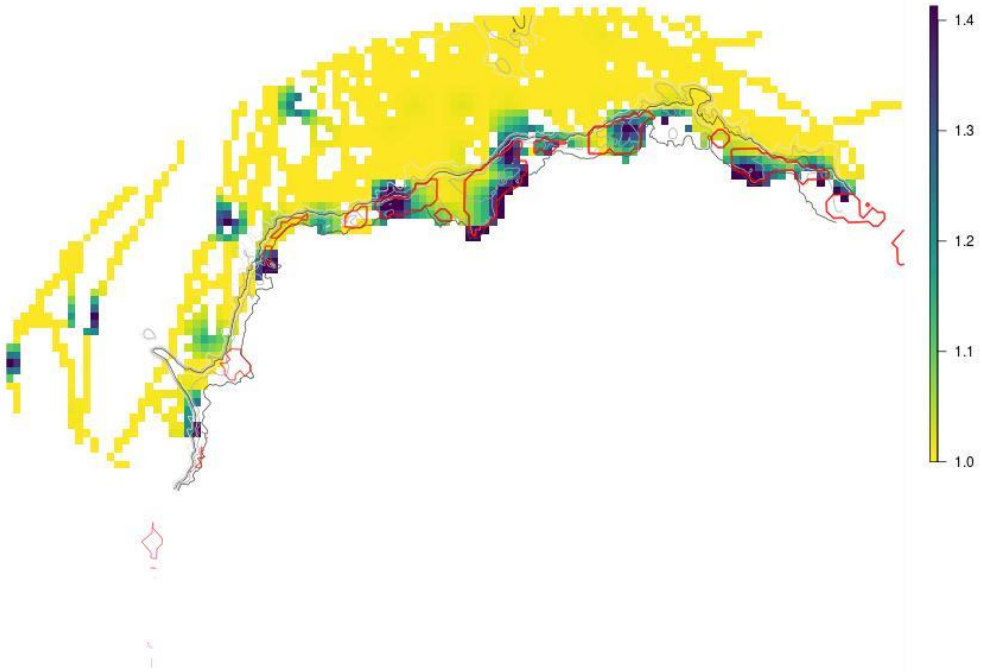

Figure 4.11. ***Geographical locations of area-restricted search behaviour.*** *Map showing mean movement behaviour as estimated using hierarchical state-space switching models (see Method). Yellow (values close to 1) indicates transit areas and darker colours indicate more encamped behaviour (indicative of area restricted search, often linked with foraging). Red polygons demarcate the post-polynya areas from Arrigo (2003)). Data shown as average values per 50 km grid cell aggregated across all individuals.*

The rate of change of body condition, represented by ΔDr_i, was higher inside than outside post-polynya areas (table 1, figure 3). There were no differences in terms of the rate of change between males and females, however Antarctic instrumented seals (predominantly males) exhibiting a high use of polynyas gained condition faster than the equivalents from Kerguelen I.

(figure 3). The rate of gain was also positively associated with area restricted search behaviour (i.e. with locations where seals exhibit a higher degree of residency).

4.4 Discussion

I have provided a quantitative analysis of the relative importance of Antarctic polynyas as foraging locations for a marine top predator in east Antarctic region. While most seals considered in our study successfully forage and recover their body condition, the benefits of earlier and larger phytoplankton blooms occurring inside polynyas translate to higher trophic levels by enhancing the success of individuals foraging inside them. By determining the changes in Drift rate and analysing the movement behaviour of the seals, we found that seals predominantly foraging inside polynyas exhibit longer periods of area-restricted search and a faster increase of their Drift rate compared with seals foraging outside polynyas. While polynyas were already known to be used by air-breathing marine predators, including elephant seals, whether it was a consequence of encroachment due to sea-ice growth, or because they acted as predictable regions of open water through the year (allowing them to access the surface) or because they were favourable areas for foraging, remained speculative.

By focusing on the Summer/Autumn period, when large areas of the Antarctic shelf remains ice-free and the seals are free to enter and leave the post-polynyas, I have avoided confounding effects due sea-ice encroachment. Rather, the results strongly support that polynyas act as specific, favourable areas embedded in the Antarctic shelf even after surrounding sea-ice has melted. Thus, the benefits of early spring phytoplankton blooms impacting the energy flux to higher trophic levels inside the polynyas remain after the sea-ice has melted, when there is no physical delimitation of the polynyas (post-polynya phase). Furthermore, elephant seals targeting post-polynyas showed area-restricted search behaviour inside them, and fast, travelling behaviour outside them (fig 3, online supplementary material figures 4-5). This particular behaviour is consistent with theoretical predictions of the optimal foraging theory, specifically when foraging occurs in patchy environments.

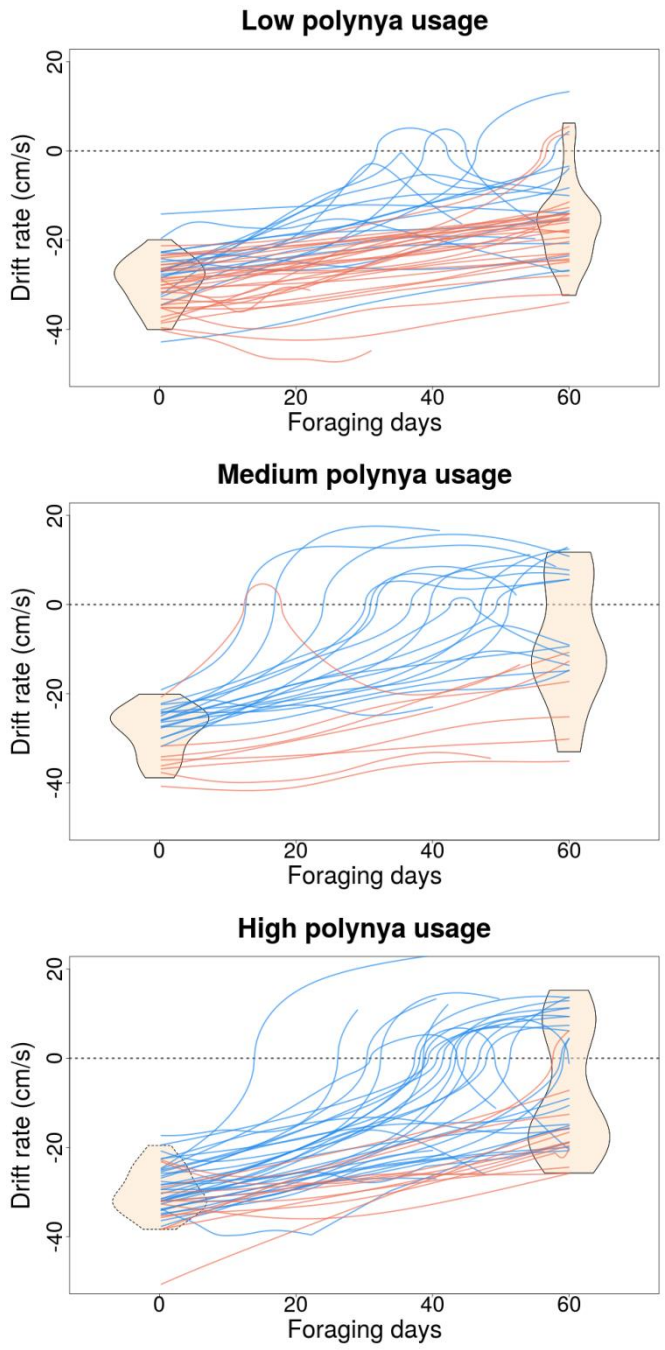

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Figure 4.12. ***Drift rate (cm s^{-1}) time series for Antarctic foraging southern elephant seals (n = 119)****. For visualization, the time series from individuals are separated according to usage of post-polynya areas: seals that spent less than 1/3 of their time inside post-polynya areas (top), between 1/3 and 2/3 of their tracked time inside post-polynya areas (middle), and more than 2/3 of their time inside post-polynya areas (bottom). Lines show the estimated drift rate from the fitted GAMS (see Method) for seals tagged at Kerguelen Is. (red, n = 50), and in Antarctica (blue, n = 69). Violin plots show the distribution of drift rates at the start and end of the 60 d period.*

I have also found a sex-specific segregation on the use of the Antarctic region. Broad scale, Antarctic foraging males visit the polynyas to forage, while Antarctic foraging females don't (online supplementary material, figure s3). A potential explanation could be the existence of sex-specific resource partitioning as absolute energetic requirements for males and females are expected to vary as a consequence of their extreme sexual dimorphism. As there is no difference in size between the females (adults) and males (juveniles, 1-5 year old) used in this study, this explanation may remain too speculative by itself. While immature males keep growing and laying down lean tissue, adult females also lay down lean tissue (in the form of foetus), thus energetic requirements for individuals of similar size classes may not be as different as expected. However previous research has already found that elephant seals travel farther south through age (Field et al. 2007a, Authier et al. 2012a) which, in fact could be masking a size effect, as Antarctic specialist that moult in the Antarctic coast belong to immature-but large size classes (Van Den Hoff et al. 2003). Besides, adult females hold tighter ties with the colonies in the sub Antarctic Islands, as they have to return to give birth to their offspring and mate (Bailleul et al. 2007b). Environmental fluctuations impact polynya and sea-ice extent (Arrigo et al. 2015, Parkinson 2019), making the winter extent of polynya and the ability to leave them highly unpredictable. The findings show that seals do not need to forage to recover their body condition. Thus, the enhanced benefit of foraging inside the polynya regions may not compensate the risks of being encroached at the time of returning back to the colony (see online supplementary material figures 4-5). Immature males, without strong bindings to the colony, can take the risk of being encroached during the winter as their ultimate goal is to growth large enough to reach breeding status. For them, the enhanced foraging success mediated by the polynya foraging may translate in faster somatic growth, especially during periods of positive buoyancy.

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4.5 Tables

Table 4.1. Fixed effects from the best fitted mixed effect models for predicting (a) polynya usage and (b) foraging success. Parameters with statistically significant slopes ($p < 0.05$) are highlighted in bold.

(a) Polynya usage

Fixed effects	**Coefficient ± SE**	***z*-value**	***p*-value**
Intercept (Kerguelen male)	-0.14 ± 0.37	-0.38	0.70
Movement behaviour	**0.65 ± 0.02**	**32.32**	**<0.001**
Δ Drift rate	**0.22 ± 0.02**	**9.23**	**<0.001**
Sex (female)	**-6.19 ± 0.64**	**-9.61**	**<0.001**
Tagging location (Antarctic)	0.74 ± 0.43	1.70	0.089

(b) Increase in Drift rate

Fixed effects	**Coefficient ± SE**	***t*-value**	***p*-value**
Intercept (Kerguelen	**0.05 ± 0.009**	**5.06**	**<0.001**

male)			
Polynya (out/in)	**0.01 ± 0.003**	**2.93**	**0.003**
Sex (female)	0.01 ± 0.013	1.04	0.30
Tagging location (Antarctic)	**0.05 ± 0.011**	**4.41**	**<0.001**
Movement behaviour	**0.01 ± 0.002**	**4.85**	**<0.001**

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4.7 Supplementary material

Table S4.1: number of seals used for the analysis. Instrumented refers to all seals initially considered for this study, while Antarctic foragers refers to seals that spend at least 50% of the foraging time 68.5 Degrees south and were considered as Antarctic foragers. Note that females were adult whereas males were immature (s4.2.1). Hence, it can be assumed that ~80% of the females would be gestating after the moult (i.e., growing a foetus) whereas males would be adding somatic tissue.

		Latitude	longitude	Instrumented		Antarctic foragers	
season	location			Female	Male	Female	Male
2008/2009	Kerguelen I.	49°20’S	70°20’E	0	9	0	4
2010/2011	Prydz bay	68°34’S	77°58’E	0	20	0	20
2011/2012	Vincennes bay	66°20’S	110°28’E	2	22	2	21
2011/2012	Prydz bay	68°34’S	77°58’E	0	20	0	18
2012/2013	Kerguelen I.	49°20’S	70°20’E	15	12	6	7
2013/2014	Kerguelen I.	49°20’S	70°20’E	6	8	2	3
2013/2014	Kerguelen I.	49°20’S	70°20’E	1	1	1	0
2014/2015	Kerguelen I.	49°20’S	70°20’E	12	11	4	5
2015/2016	Prydz bay	68°34’S	77°58’E	0	2	0	2
2015/2016	Kerguelen I.	49°20’S	70°20’E	10	2	3	1
2016/2017	Prydz bay	68°34’S	77°58’E	0	6	0	6

2016/2017	Kerguelen I.	49°20’S	70°20’E	8	2	2	2
2017/2018	Kerguelen I.	49°20’S	70°20’E	13	11	4	6
	Total			67	126	24	95

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Table S2. Candidate models for polynya usage, ordered by Delta AICc. Best two models have a very similar AICc value (Delta AICc = 0.96) and a cumulative summed weight of 100%. That makes them equivalent (Burnham and Anderson 2002). The difference between both models formulation is the inclusion of location as a fixed effect in the best model. Its effect has no statistical significance (ADD p-value), and there is not a big difference between the estimate of the rest of the effects (besides the intercept).

Intercept	locKA	I(scale(b))	I(scale(dif))	sex	df	logLik	AICc	delta	weight
-0.1393	+	0.6536	0.2195	+	6	-10388.8	20789.67	0	0.609
0.3804		0.6537	0.22	+	5	-10390.3	20790.55	0.884	0.391
-2.5818	+	0.6533	0.2193		5	-10432.1	20874.17	84.498	0
-0.1786	+	0.6835		+	5	-10442	20893.94	104.267	0
0.3797		0.6837		+	4	-10443.6	20895.26	105.59	0
-0.8023		0.6535	0.2205		4	-10447.3	20902.5	112.833	0
-2.6125	+	0.6833			4	-10485.1	20978.16	188.494	0
-0.8069		0.6836			3	-10500.7	21007.43	217.76	0
-0.1313	+		0.3478	+	5	-10935	21879.93	1090.265	0
0.431			0.3484	+	4	-10936.5	21880.92	1091.254	0
-2.6753	+		0.3476	NA	4	-10977.2	21962.47	1172.801	0
-0.8057			0.3489	NA	3	-10992.4	21990.78	1201.111	0
-0.198	+			+	4	-11059.3	22126.56	1336.892	0
0.4299				+	3	-11061.1	22128.27	1338.598	0
-2.7309	+				3	-11101.3	22208.64	1418.972	0

-0.815					2	-11117.2	22238.44	1448.775	0

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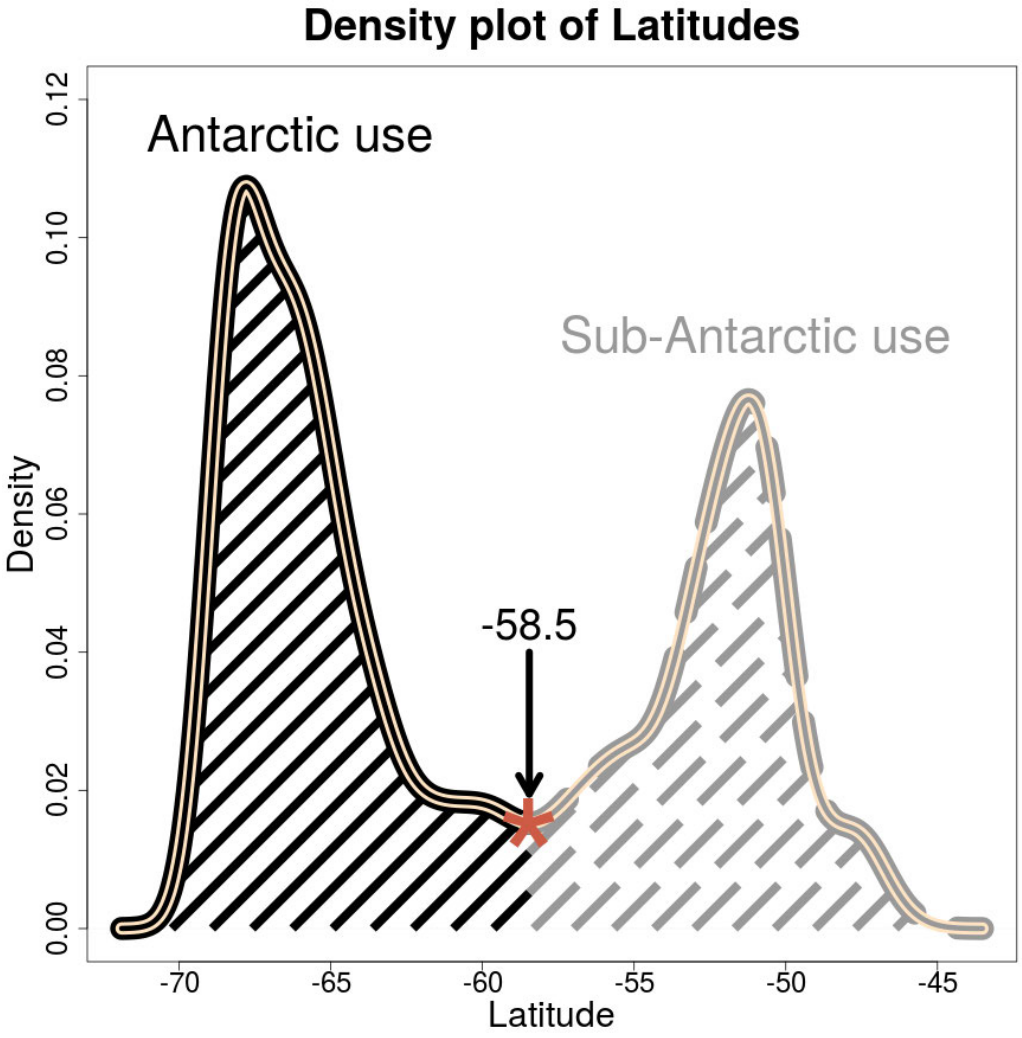
Table S3. Candidate models for foraging success ordered by Delta AICc. Best two models have a similar AICc value (Delta AICc = 0.93) and together they have a cumulative value of 95.6%.

Intercept	locKA	polynya	I(scale(b))	sex	df	logLik	AICc	delta	weight
0.0538	+	+	0.0108		7	23152.05	-46290.1	0	0.587
0.0476	+	+	0.011	+	8	23152.58	-46289.2	0.931	0.369
0.0569	+		0.0113		6	23148.07	-46284.1	5.962	0.03
0.0528	+		0.0115	+	7	23148.3	-46282.6	7.491	0.014
0.0777		+	0.0112		6	23142.71	-46273.4	16.676	0
0.0812		+	0.011	+	7	23143.5	-46273	17.085	0
0.0514	+	+			6	23140.83	-46269.7	20.426	0
0.0472	+	+		+	7	23141.06	-46268.1	21.982	0
0.0871			0.0115	+	6	23139.13	-46266.3	23.826	0
0.0828			0.0118		5	23137.74	-46265.5	24.609	0
0.0548	+				5	23135.67	-46261.3	28.751	0
0.0531	+			+	6	23135.71	-46259.4	30.681	0
0.0817		+		+	6	23131.99	-46252	38.119	0
0.077		+			5	23130.6	-46251.2	38.885	0
0.0883				+	5	23126.59	-46243.2	46.914	0
0.0827					4	23124.35	-46240.7	49.385	0



1640

1641 **Figure S1. Density distribution of Latitudes transmitted from the seal tags**. The
1642 minimum density value in-between the two peaks occurs at 58.5 degrees south. This value is
1643 further used as a threshold to classify seals as Antarctic vs non Antarctic foragers.

1644

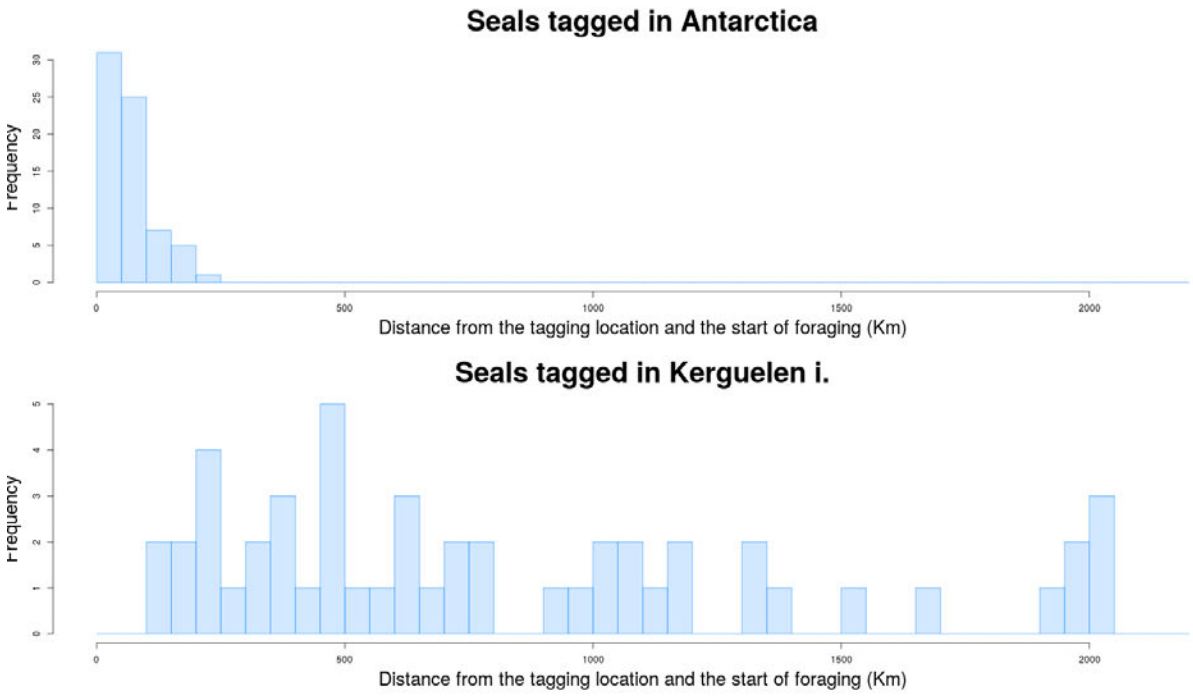


Figure S2. Distances from the deployment location and the start ofdrift diving. Histograms of the distances from the tagging location to the start of foraging (considered at the time of performing the first drift dive) seals instrumented in Antarctica and in Kerguelen I.

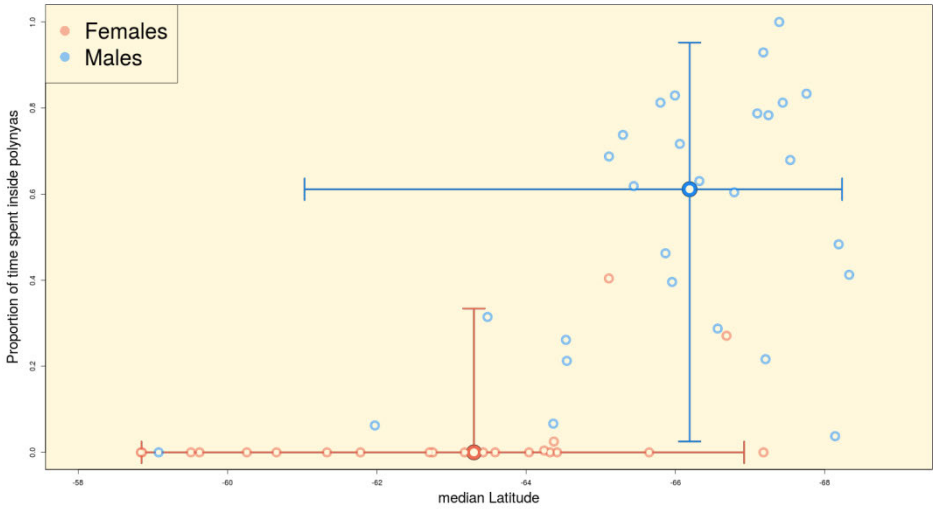
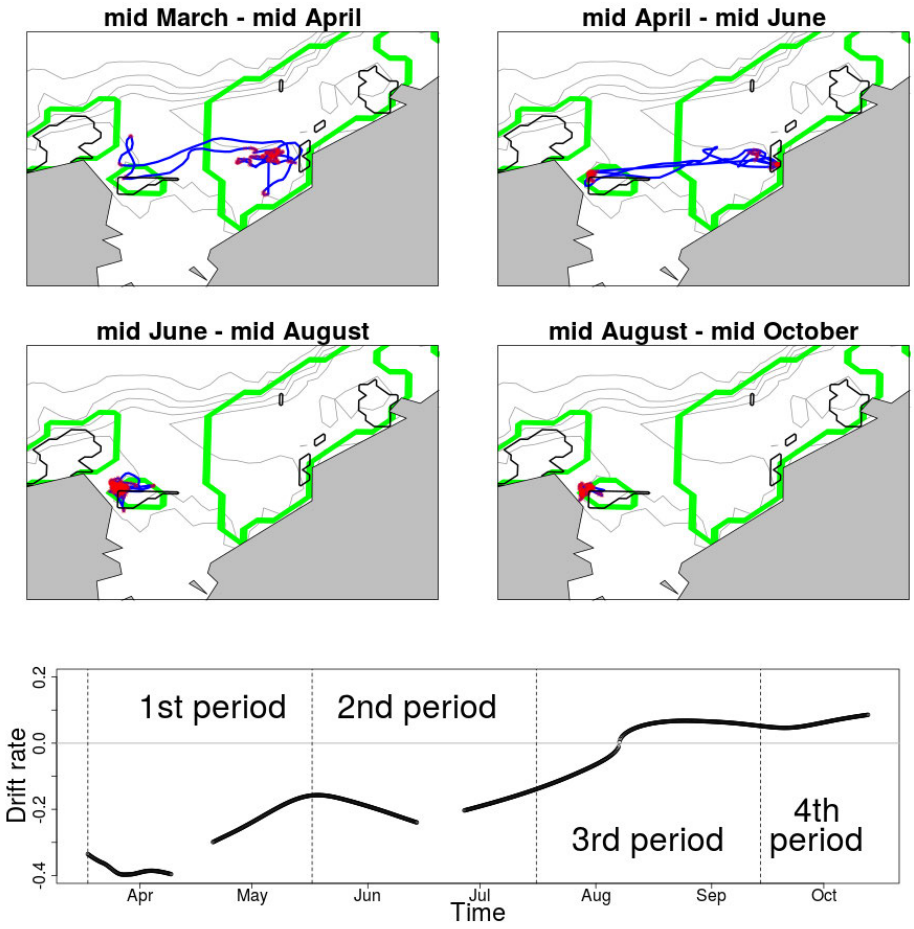


Figure S3. Relationships between latitude and time spent inside polynyas. Plot of the median latitude and the proportion of time spent inside the post-polynya areas during the 60-day period of seals instrumented in Kerguelen I. Even when there is an overlap on the median latitude between males and females, the latter makes a much less use of the post-polynya areas.



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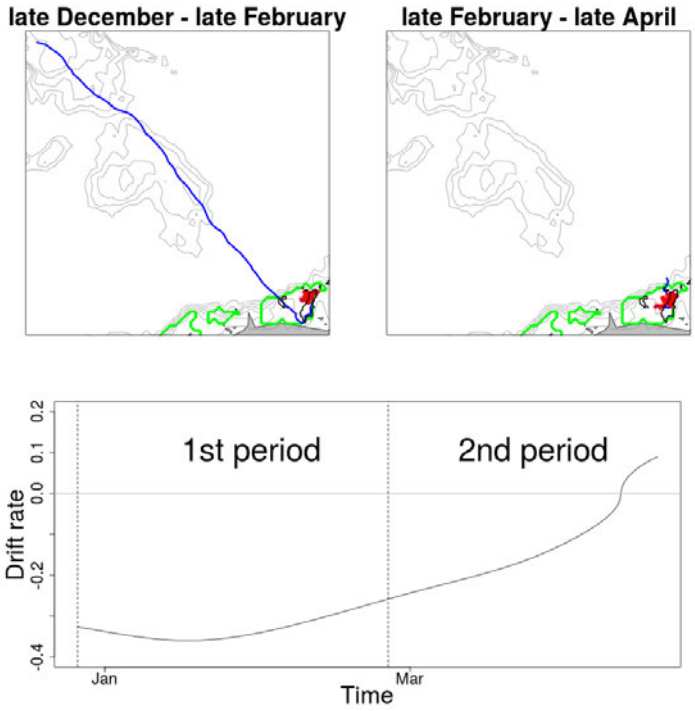
1659

1660 **Figure S4. Complete foraging track of a polynya specialist (immature male)**
1661 **instrumented in Antarctica (Prydz bay) and its drift rate time series.** Each map
1662 represents 60-day period (thus, the first map coincides with our temporal coverage). Blue line
1663 represents transit period and red dots area restricted search. During late summer-early winter
1664 the seal moves Prydz bay and McKenzie polynyas, concentrating the foraging inside them.
1665 As winter advances (from mid-June to mid-October) the seal remains performing area
1666 restricted search in a very small location of McKenzie polynya, suggesting that it has been
1667 encroached by sea-ice. Drift rate time series shows periods of gain and loss, but in the long
1668 run it gained body condition and became positively buoyant during the winter, while foraging
1669 inside the polynya.

1670



1671

1672 **Figure S5. Polynya specialist (immature male) instrumented in Kerguelen I**. This seal
1673 has travelled straight from Kerguelen I. to Farr bay polynya but started to forage close to the
1674 colony. On transit to the Polynya the seal is losing body condition, suggesting that it is
1675 prioritizing the earlier arrival to the polynya over foraging. Once inside the polynya it shows
1676 a fast recovery of body condition. This tag transmitted for ~4 months, but the last
1677 transmissions show it departing from the polynya, suggesting encorachment avoidance.
1678

Chapter 5 Investigating relationships between dive behaviour and body condition in a continuous deep diver

5.1 Introduction

Acquiring resources is a central task for heterotrophic organisms. How successful they are will be a key determinant of their fate, governing how long they might live, their rate of growth, and the amount of energy that can be placed into reproduction without comprising future survival; ultimately determining individual fitness (Stearns 1992).

Prey fields are not uniformuniform in space and time (Fauchald 1999), requiring search strategies to maximize the chance of finding appropriate prey fields (Sims et al. 2008). Foraging theories predict how an animal should respond to variations in their immediate environment, alternating periods searching for prey patches with periods hunting prey inside those patches, in such a way that they keep foraging until the prey capture rate becomes reduced as a result of patch depletion, and switch into a prey searching behaviour until another profitable patch has been found (MacArthur and Pianka 1966, Pyke et al. 1977). Theory also predicts patch abandonment linked to prey depletion (Charnov 1976, McNamara 1982), although there may be other constraints forcing foragers to leave a good quality patch, such as offspring provisioning, or physiological constraints (Houston and McNamara 1985, Stephens et al. 2008). This switching behaviour can generate a pattern of horizontal displacements with two main modes. A transit behaviour, characterized by fast, directed movements, and a second behaviour characterized by slow, less directed movements; the latter is often referred to as area-restricted search (ARS) potentially linked to foraging activities. These behaviours are often analysed using empirical approaches such as first passage time (Fauchald and Tveraa 2003), or more recently, process-based state-space models (Patterson et al. 2008, Jonsen et al. 2013).

Diving marine foragers add a third dimension to their searching strategies as their prey fields are patchily distributed throughout the water column (Fauchald et al. 2000). For air-breathers, the need to return to the surface to re-oxygenate adds further constraints to their foraging behaviour (Boyd 1997, Stephens et al. 2008, Houston 2011). Hence the foraging of air-breathing marine predators is commonly approached through study of their diving behaviour, classically focusing on widely available two-dimensional time-depth profiles.

For analyses of time-depth dive profiles, a commonly studied measure is the dive bottom time (Carbone and Houston 1996, Thompson and Fedak 2001). The bottom time of a dive

can be broadly defined as the duration remaining after exclusion of the descending and ascending phases. Common measures of bottom time linked with foraging behaviour include both the absolute duration of the bottom phase, or the proportion of time spent in the bottom phase in relation to the total dive duration (Thompson and Fedak 2001, Viviant et al. 2016). Though similar, they reflect different behaviour. The first one often links to increasing the diving effort, while the second one links to optimizing the diving effort. Increasing the diving effort might be expected to happen when individuals find a good foraging patch but optimizing the diving effort has broader implications as the costs associated with underwater movements are strongly related to the buoyancy (body condition) of the animals (Williams et al. 2000, Aoki et al. 2011, Richard et al. 2014a).

Elephant seals spend up to ten months per year at sea (Hindell et al. 1991b, Boeuf et al. 2000), with adults only visiting land twice to breed and to moult (with the exception of some individuals, probably males, that may have a short mid-winter haul-out). At sea, they perform long (20-30 min on average, sometimes beyond 1 hour of length), deep (higlyhighly variable among individuals, with an average of 400—500 m, and up to 2000 m) dives followed by sort (1-3 min) intervals at the surface to breathe (Hindell et al. 1991b). Hence, the majority of their at-sea period is spent underwater. Elephant seals are wide-ranging generalist consumers (Bradshaw et al. 2003, Naito et al. 2013), known to adopt both benthic and pelagic diving strategies, in shelf and oceanic environments respectively (Mcconnell et al. 2004, Hindell et al. 2016). In these different environments, the prey fields are likely to be quite different. Large, solitary benthopelagic, energy-dense fishes inhabit the benthic environments of shelf regions and seamounts throughout the Southern Ocean (Péron et al. 2016, Burch et al. 2017). In oceanic waters the mesopelagic layers are occupied by mixed aggregations of medium- to large-sized fishes and squids, representing an energy-rich source of prey. From the perspective of predation threats, shelf regions are also key habitat for the few elephant seal predators, the southern sleeper sharks (*Somniosus antarcticus*) and killer whales (*Orcinus orca*), the only other apex predator that a southern elephant seal may face in the Southern Ocean.

In this chapter, I again utilize the approaches developed in Chapters 1 and 2 to track the drift dives of elephant seals. From the periods when seals passively drift through the water column the drifting rate is calculated, giving information on body condition and its changes through time, which are related to the net energy intake; the real outcome (natural currency) of foraging. This chapter aims to explore the nature of relationships between diving behaviour

and body condition, and hownet energy gain for elephant seals respond to changes with respect to different prey fields. The two questions specifically addressed here are: i) can diving behavioura; metrics act as predictors for seal *body condition* (absolute drift rate), and ii) particularly for benthic or pelagic foraging strategies, can diving behavioural metrics be used as predictors of relative changes in drift rate. Of key interest, is if there are constraints that may be linked to the specific life history characteristics and therefore priority choices faced by immature males and adult females.

5.2 Material and methods

5.2.1 Seal instrumentation

The Australian Integrated Marine Observing System in collaboration with the French Centre for National Scientific Research has tagged over two hundred southern elephant seals in the Southern Ocean, at Isles Kerguelen as well as Prydz and Vincennes Bays (the latter two located in East Antarctica). Seal capture, handling and instrumentation protocols have been described elsewhere (McMahon et al. 2000a). Each seal was instrumented with a Satellite-Relayed Data logger (CTD-SRDL, Sea Mammal Research Unit, University of St. Andrews). These instruments record time, depth, temperature and conductivity every 8 s and transmit a compressed version of the dataset via the Argos satellite system. To overcome the limited bandwidth available in the Argos system, time-depth information is processed on-board the tag. Each dive is summarized using a broken-stick algorithm before transmission retaining four primary inflection points as well as the start time and duration of dives, and a random sub-set of them is transmitted. Argos location estimates are also estimated at each uplink using Doppler shift (Argos 2011).

5.2.2 Track processing

Horizontal movement paths of seals were reconstructed from the sparse, error-prone, and irregularly obtained Argos position estimates, using hierarchical state-space behavioural switching models (Jonsen 2016) implemented in the R package *bsam* (Jonsen et al. 2005). This approach filters erroneous locations and provides position estimates, together with the associated uncertainties, at regular time intervals (in this case at a 6 h time step). The state switching process model also provides a behavioural state estimate based on the movement parameters for direction (turn angle) and move persistence (the autocorrelation in speed and direction). Two states are estimated: transit, where the seal makes fast directed travel, and area restricted search (ARS), where the seal undertakes slower travel within a more localised region with many changes in direction. As the state space models return the posterior estimate for the mean behavioural state on a continuous scale (from 1 to 2), but actually fit a discrete movement behaviour (transit vs ARS), a threshold of 1.3 is considered to differentiate transit and ARS behaviours.

5.2.3 Drift dive identification

Drift dives have a characteristic long, inactive phase where the vertical displacement of the seal through the water column largely depends on the seal's buoyancy (Biuw et al. 2003).

Identification of these drift dives, and calculation of drift rates during the passive phase allows estimation of the buoyancy of the seal and how this changes through time. We processed the summarized dive profile information provided by the CTD-SRDL tags following the approach introduced by Arce et al. (2019a) in the R (R Core Team 2018) package *slimmingDive* (Arce et al. 2019a). This package makes an initial filtering process of dives and assigns likelihood for any remaining dive being a drift dive; for this study we consider drift rate estimates (cm s^{-1}) only from dives that have at least 95% probability of being true drift dives.

5.2.4 Dive behaviour metrics

The SRDLs transmit the BSM inflection points together with other dive measures, like dive duration (min), maximum dive depth (m), and post-dive surface interval duration (min) for a randomized selection of all dives made by individual seals (Photopoulou et al. 2015). Preliminary analyses were undertaken considering a wide suite of candidate behavioural metrics, but here I report on five specific and derived metrics:

(i) **Descent rate** of vertical displacement calculated by dividing the depth at the first inflection point by the time taken to reach that point.

(ii) **Ascent rate** of vertical displacement calculated by dividing the depth of the last inflection point by the time taken to return from there to the surface.

(iii) Proportional **bottom time -** the time spent at the bottom of the dive (calculated as the duration of the period between the first and last inflection points) as a proportion of the total dive duration.

(iv) **Dive residual** – calculated as the residuals from a regression model of the log dive duration against the log maximum dive depth for each seal (*dres*). This has been used to provide a measure of relative dive effort (Bestley et al. 2015), where dives with a positive residual are relatively long for a given dive depth, and those with negative residuals are relatively short.

(v) **Ratio residual** - the ratio between the residual of the last inflection point extracted during the dive summarization and the maximum dive depth (*ratiores*). This provides a measure of diving complexity that remains not well captured by the broken-stick algorithm. This residual was calculated using a reverse broken-stick algorithm implemented in *slimmingDive*.

Each dive was also allocated to one of two foraging types based on its proximity to the ocean floor. “Benthic” dives were those with maximum depths within 20 m of the seafloor, and all other dives were categorised as “pelagic”. Locations at each dive timestamp were estimated using linear interpolation along the estimated path from the SSMs, and the bathymetry at these locations were extracted from GEBCO14 (Sandwell et al. 2002).

5.2.5 Integration of location, body condition and dive behaviour

As seal locations were calculated at 6 h intervals, each dive metric was averaged for all dives occurring in the 3 h preceding and following each location estimate. Averaged metrics are abbreviated as follows: *mdur* (averaged dive duration), *msur* (averaged surface duration), *beff* (proportion of dive duration spent at the bottom of the dive), *mratiores* (averaged *ratiores*), *mdres* (averaged *dres*), *msp* (averaged descending speed), *mas* (averaged ascending speed), *bf* (horizontal behaviour as factor, ‘transit’ and ‘ARS’). Inspection of correlation matrices ensured no substantial collinearity amongst these variables (typically Pearson’s $r < 0.45$, Supplementary material figure S1).

Drift rates were similarly averaged to associate one body condition estimate with each location. Where drift dives were detected in adjacent 6 h periods, the change in drift rate (Δdrift rate) was calculated over that interval. Foraging type (benthic/pelagic) for each location was assigned according to the most common type within the 6 h period. Each metric was calculated separately for benthic and pelagic dives. The final analysis included all seals that met the following data criteria: performed at least ten drift dives overall, with sufficient adjacent observations to contribute at least 4 Δdrift rate estimates.

5.2.6 Mixed-modelling approach

Two statistical analyses were used for investigating:

(i) Diving behavioural metrics as predictors for seal body condition

Here, *Drift Rate* is the response variable and the fixed effects were the dive metrics described above. To account for likely different responses occurring due to positive and negative buoyancy the analysis was performed separately to the dataset split based on the buoyancy sign. All the numerical fixed effect variables were scaled (centered to have mean = 0 and sd = 1) after the split by sign. We included seal identity as a random effect, and a continuous time autocorrelation (corCAR1) to account for the strong temporal dependency in the data. We fitted linear mixed models using the R package *nlme* (Pinheiro et al. 2019),

and used the package *MuMIn* (Bartoń 2018) 'dredge' function to assess the top models (all those with ΔAICc < 2) and perform full model averaging to obtain the final coefficient estimates

(ii) Diving behaviour as predictors of drift rate changes for benthic or pelagic foraging strategies

This part of the analysis focussed upon the first 60 days of the post-moult foraging trips, when the seals exhibit the most pronounced changes in body condition (see Chapter 3). The start of the foraging trip is identified when the seals performed the first drift dive. At the start of the post-moult trip, seals typically have low body condition. Later in the foraging trips there may be other confounding factors (such as the increasing size of the foetus in pregnant females, or the somatic growth of the males). The model structure and fitting were the same as described above, except here the Δdrift rate (from one 6 h period to the next) is the response with the suite of dive metrics again as predictors, and the inclusion of sex as an interaction, additive fixedterm. Separate models were fit to benthic and pelagic foraging behaviours and the numerical predictors were scaled separately for each group.

5.3 Results

Data processing retained 143 out of 195 seals (39 females and 104 males) that transmitted diving information for an average of 160 ± 79 days. During the post-moult trips, seals transmitted a total of 1,204,916 individual dives; of these, 23,776 (2%) were identified as drift dives. Transmitted dives (excluding those identified as drift dives) constituted a total of 78,208 6 h diving periods of which 12,108 (15%) were classified as benthic and 66,077 (84%) as pelagic. The state-space modelling approach estimated 37,982 (49%) of the 6 h locations represented area-restricted search movements, and 40,226 (51%) indicated transit behaviour. From the 78,208 6-hour gathered periods, 13,788 (17.5%) and 2,796 (3.5%) contained drift rate and Δdrift rate information, respectively, and were used for modelling purposes. The periods of negative buoyancy are widespread along the seals tracks (figure 5.1-A), while the periods of positive buoyancy are somewhat restricted to the Antarctic shelf and the Kerguelen plateau, and in between them (Figure 5.1-B). Benthic behaviour is restricted to relative shallow areas (Antarctic shelf and Kerguelen plateau) as the ocean floor has to be below the diving limits of the seals in order to be able to forage benthically (fig 5.1-C) while the pelagic behaviour has been found in both shallow and deep waters (Figure 5.1-D)

Only 3 out of 104 males (<3%) exhibited no benthic behaviour, in comparison with 17 out of 39 females (44%). Of those individuals which did exhibit benthic diving behaviour, this represented on average 24 ± 16% of their time for males and 7 ± 11% for females (Supplementary material figure S2). Females were subsequently removed from the dataset of benthic behaviour prior to analysis

5.3.1 Body condition in relation to diving behaviour

The mixed models showed significant but opposite effects between periods of positive and negative buoyancy for three dive metrics. Positive coefficients in the model for negatively buoyant seals (Table 5.1) indicated that better body condition (i.e. drift rates approaching neutral buoyancy) was associated with longer dives (*mdur*, Figure 5.2), more efficient dives (with proportionally longer bottom time, *beff*, Figure 3*)* and more complex dives (*ratiores*, Figure 5.4). This pattern reverses during periods of positive buoyancy, where these coefficient estimates were all negative (Table 5.1, Figures 5.2-4). For positively buoyant seals, better body condition (*i.e.* more positive drift rates) was associated with shorter, less efficient and less complex dives (Figures 5.2-4). Additionally, for negatively buoyant seals there was a significant negative association with the diving residual (*dres*), indicating higher drift rates were linked with relatively short dives for a given depth (i.e., more negative dives residuals). Finally, for positively buoyant seals, a reduction in the body condition was found to be significantly related to an increased probability of being in 'transit' behaviour. No significant relationship was found for either averaged descending speed (msp) or averaged ascending speed (mas).

5.3.2 Predicting drift rate changes for benthic/pelagic strategies

No significant relationship was found between the Δdrift rate and any of the considered diving metrics during the benthic behaviour (Table 5.2, Figure 5.1). During pelagic diving behaviour, a significant positive relationship was identified between the Δdrift rate and the descending speed was found (Table 5.2). Although, ARS behaviour was four times more common during benthic behaviour than during pelagic behaviour. For the pelagic foraging, there were no differences among sexes, and for the considered periods movement behaviour was not significantly associated with foraging success in either model.

5.4 Discussion

The modelling frameworks have found contrasting effects and relationships between the body condition, foraging success, and a number of summarised dive metrics. Some of the results that have been found in previous analysis were carried out with the aid of high-resolution accelerometers. For example, Richard, Vacquié-Garcia, et al. (2014) found faster speeds in both transit phases (descending and ascending periods) and show more sinuosity inside the bottom of the dives, congruent with Miller et al. (2012). Here, I have found both significant effects on the descending phase and in the sinuosity of the dives, but not on the ascending speed.

Air-breathing marine predators can be broadly classified in two distinctive groups. So-called 'divers' (e.g., penguins, cormorants) spend a large amount of time at the surface, with diving time focused upon foraging. So-called 'surfacers' (e.g., elephant seals, sea-turtles) spend most of the time diving, returning to the surface briefly to re-oxygenate (Hindell et al. 1991b, Watwood et al. 2006). In the first group, a great proportion of the time spent underwater is likely to be associated with foraging/searching than is the case for 'surfacers', and thus, changes in foraging conditions are expected to strongly influence their diving behaviour. For example, divers may choose to extend their bottom time at the expense of longer surface recovery periods. Or, single-prey handlers may actually shorten their dives as a consequence of higher prey-density – due to earlier capture success. Divers may also set a threshold at which, if no prey is encountered, the animal may give up and return to the surface (Houston 2011). However, 'surfacers' are not necessarily expected to show several of these behaviours. Rather, they would optimize their dives from the point of view of continuous diving behaviour. That is, they will keep diving even if there are not searching for prey, as most of their activities will be placed underwater. That helps explaining why most of the responses are found to be linked to the body condition and not to the changes in Drift rate.

5.4.1 Body condition

Experimental approaches via buoyancy manipulation together with time-depth recorders and accelerometer data in marine mammals have shown that their diving behaviour is strongly influenced by the body condition. Specifically, there is an increase of horizontal swimming effort as the body condition deviates from neutral buoyancy (Sato et al. 2003, 2013, Aoki et al. 2011). The first modelling approach presented shows that longer (Fig. 5.2), more efficient (Fig. 5.3) and complex dives (Fig. 5.4) tend to be associated with body conditions close to

neutral buoyancy, confirming that neutral buoyancy is the most efficient body condition for elephant seals. At the same time, dives closer to neutral buoyancy tend to be shorter for a given depth (figure 5,)Miller et al. 2012, Adachi et al. 2014). A plausible explanation is that in these circumstances, seals are making more intense searching dives, as shown by the increasing dive complexity (figure 5.4), and thus, the dive duration became shorter.

This modelling framework could potentially be used to infer the body condition via the relevant metrics, but the opposite effects found between periods of positive and negative buoyancy prevents a straightforward use. Globally, longer, efficient, and complex dives are associated with better body condition, but this relationship reverts if the seal became positive buoyant. This modelling framework would be unable to discriminant a positive buoyant seal (i.e. a very successful forager) from a negative buoyant seal (potentially less successful forager) as the condition deviates both from neutral buoyancy. It could, however use in specific circumstances like the post-breeding trips, or the earlier parts of their post-moult trips, when seals are negative buoyant. It would, however, require a careful examination of the generated time-series of body condition

5.4.2 Response to foraging success

The lack of response to an increase on the foraging success for benthic foraging can be explained by the likely prey fields. Automated recording devices on deep long lines set for toothfish in the Kerguelen plateau have record non-lethal interactions between the lines and elephant seals at deeps above 1000 m. depth (van den Hoff et al. 2017). Toothfish are large, energy dense benthopelagic fish, known to be solitary and resident. If toothfish or similar species are taken by elephant seals while benthic foraging, then, a prey capture event may not trigger any expected modification of their behaviour. Targeting solitary and scattered distributed prey means that a successful catch does not increase the probability if finding a second item. We hypothesise that seals will not increase for example descent speeds for solitary prey, since the probability of encounter prey is independent for each dive. Energy gain per capture is also quite high for prey type such as toothfish and icefish. Such an hypothesis could be tested using accelerometry measurements to asses how often prey are encountered within benthic and pelagic environments.In the constrating case for pelagic foraging, elephant seals are known to use schools of pelagic fishes/squids (Authier et al. 2012b), as seen in both diet stable isotopes and animal-borne cameras (Naito et al. 2013). In these circumstances, finding prey during a dive may increase the chances of finding further prey on that dive. Accelerometry data is available for pelagic foragers and shows many prey

encounters per dive (Goulet et al. 2020). As these schools are highly mobile and may actually respond to predation events, by dispersing or fleeing, in these circumstances, several behavioural responses are possible. Here, the most likely response should be an increase in descent speed to return to the prey path quickly, as identified whithin analysis. Another expected response could be minimizing the time they have to spend out of the patch for re-oxygenizing, however this was not supported by the results.

Thus, elephant seals are able to exhibit different behaviours in different environments accordingly with their expectations.

5.5 Tables

Table 5.1. Results from the mixed-effects models examining body condition (using drift rate). Separate models were fit to the positive (n = 1070 time periods) and negative (n = 10769) buoyancy data. Estimates are obtained using multi-model inference across all models within ΔAIC<2 of the lowest AIC; reported here are the full model averaged coefficients across these selected models. Parameters with statistically significant slopes ($p < 0.05$) are highlighted in bold. NA indicates predictor was not retained in any of the final models. Averaged metrics are abbreviated as follows: *mdur* (averaged dive duration), *msur* (averaged surface duration), *beff* (proportion of dive duration spent at the bottom of the dive), *mratiores* (averaged *ratiores*), *mdres* (averaged *dres*), *msp* (averaged descending speed), *mas* (averaged ascending speed), *bf* (horizontal behaviour as factor, 'transit' and 'ARS').

	Negatively buoyant			Positively buoyant		
Dive metrics	Coefficient	Std. Error	Pr(>|z|)	Coefficient	Std. Error	Pr(>|z|)
(Intercept)	**-0.2095**	**0.0035**	**0**	**0.077**	**0.0054**	**0**
beff	**0.0019**	**0.0006**	**<0.001**	**-0.0197**	**0.0031**	**0**
mdur	**0.0024**	**0.0008**	**0.004**	**-0.0101**	**0.0031**	**0.0014**
mdres	**-0.0019**	**0.0006**	**0.001**	-0.0004	0.0014	0.7969
mratiores	**0.0014**	**0.0006**	**0.024**	**-0.0056**	**0.0026**	**0.0374**
msp	-0.0009	0.0008	0.291	0.0003	0.0015	0.8231

bf-transit	-0.0001	0.0009	0.887	**-0.014**	**0.0061**	**0.0224**
mas	0	0.0003	0.907	-0.003	0.0036	0.4023
msur	NA	NA	NA	NA	NA	NA

1991

1992

1993

Table 5.2. Results from the mixed-effects models examining changes in body condition (Δdrift rate). Separate models were fit to the benthic (n = 268 time periods) and pelagic (n =1110) foraging data. Estimates are obtained using multi-model inference across all models within ΔAIC<2 of the lowest AIC; reported here are the full model averaged coefficients across these selected models. Parameters with statistically significant slopes ($p < 0.05$) are highlighted in bold. NA indicates predictor was not retained in any of the final models.

Dive metrics	Benthic behaviour			Pelagic behaviour		
	Coefficient	Std. Error	Pr(>|z|)	Coefficient	Std. Error	Pr(>|z|)
(Intercept)	-0.0057	0.0081	0.484	**-0.0163**	**0.005**	**0.0012**
msp	0.002	0.0034	0.557	**0.0077**	**0.002**	**0.0001**
mas	0.0017	0.0036	0.638	NA	NA	NA
mdur	0	0	0.776	NA	NA	NA
bf	0.0003	0.0015	0.826	0.0007	0.0012	0.594
mdres	0.0003	0.0019	0.875	-0.0018	0.0028	0.5125
mratiores	0.0012	0.0087	0.891	0.0191	0.0154	0.214
msur	0	0	0.943	0	0	0.592
beff	NA	NA	NA	0.0074	0.0076	0.3289

5.6 Figures

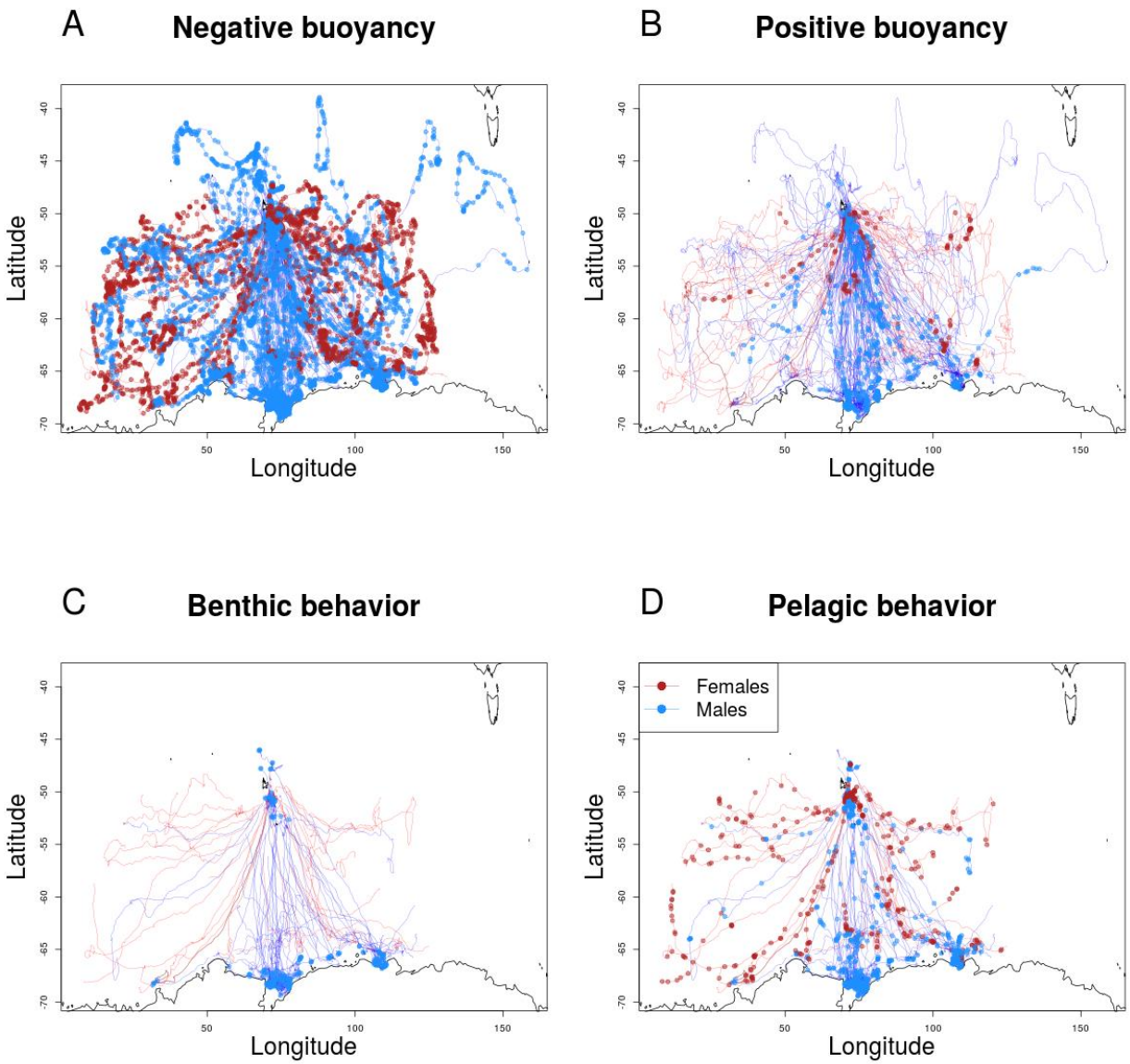
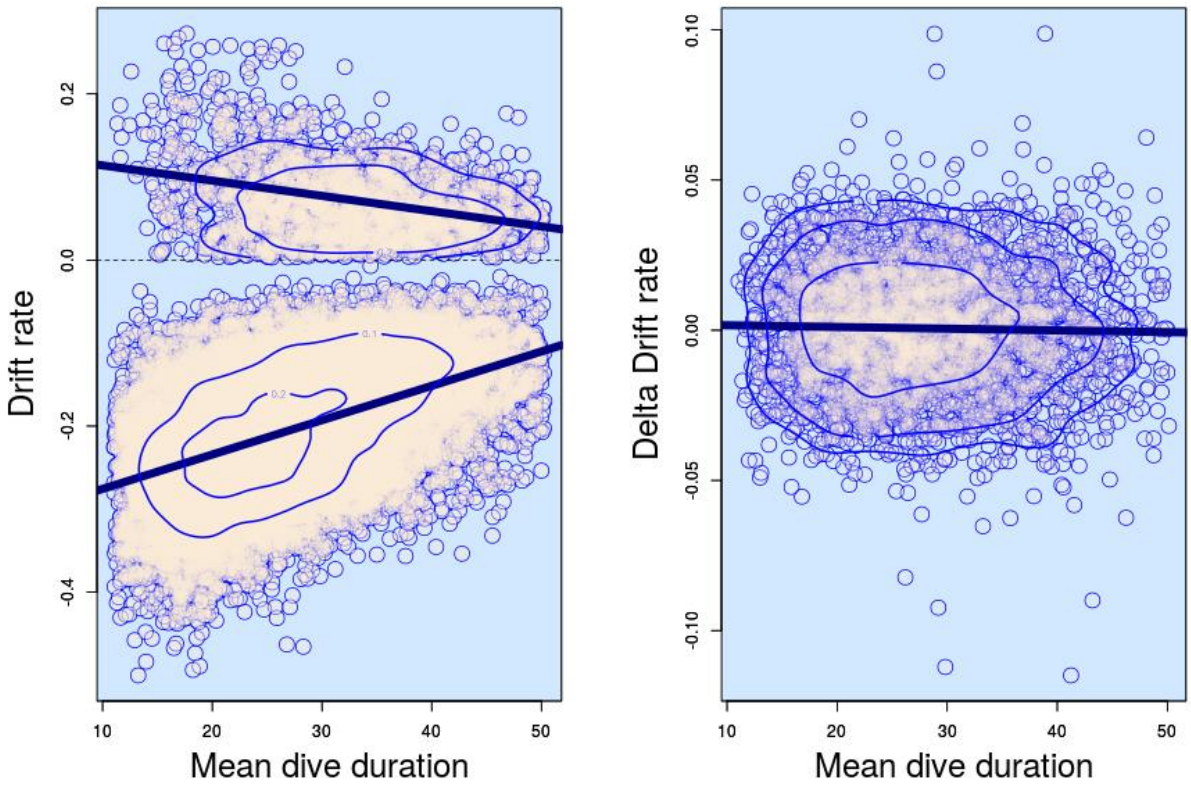


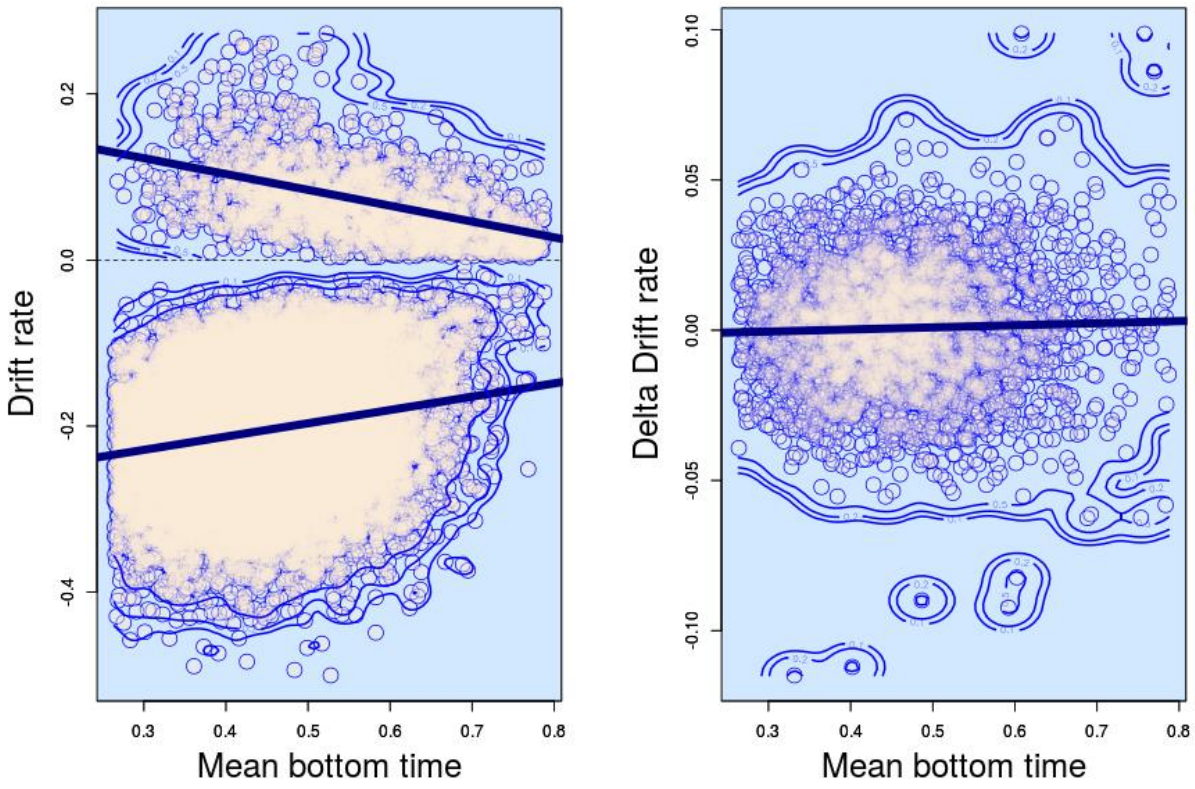
Figure 5.1. Spatial distribution of the point locations used for fitting the four global models. A: Spatial distribution of the periods of negative buoyancy (N = 10769), B: Spatial distribution of the periods of positive buoyancy (N = 1070), C: spatial distribution of the benthic behaviour (N = 268), and D: spatial distribution of the points of pelagic behaviour (N = 1110).



2012

2013 **Figure 5.2. Relationships between the body condition (drit rate) and Δdrift rate with the**
2014 **mean dive duration**. Fitted least square regressions are included to reveal the nature of the
2015 relationships between them. Drift rate was further split in accordance with the drift rate sign
2016 to allow opposite relationships to be revealed.

2017



2018

2019 **Figure 5.3. Relationships between the drit rate and the Δdrift rate and the mean bottom**
2020 **time (*beff*).** Fitted least square regressions are included to reveal the nature of the
2021 relationships between them. Drift rate was further split in accordance with the drift rate sign
2022 to allow opposite relationships to be revealed

2023

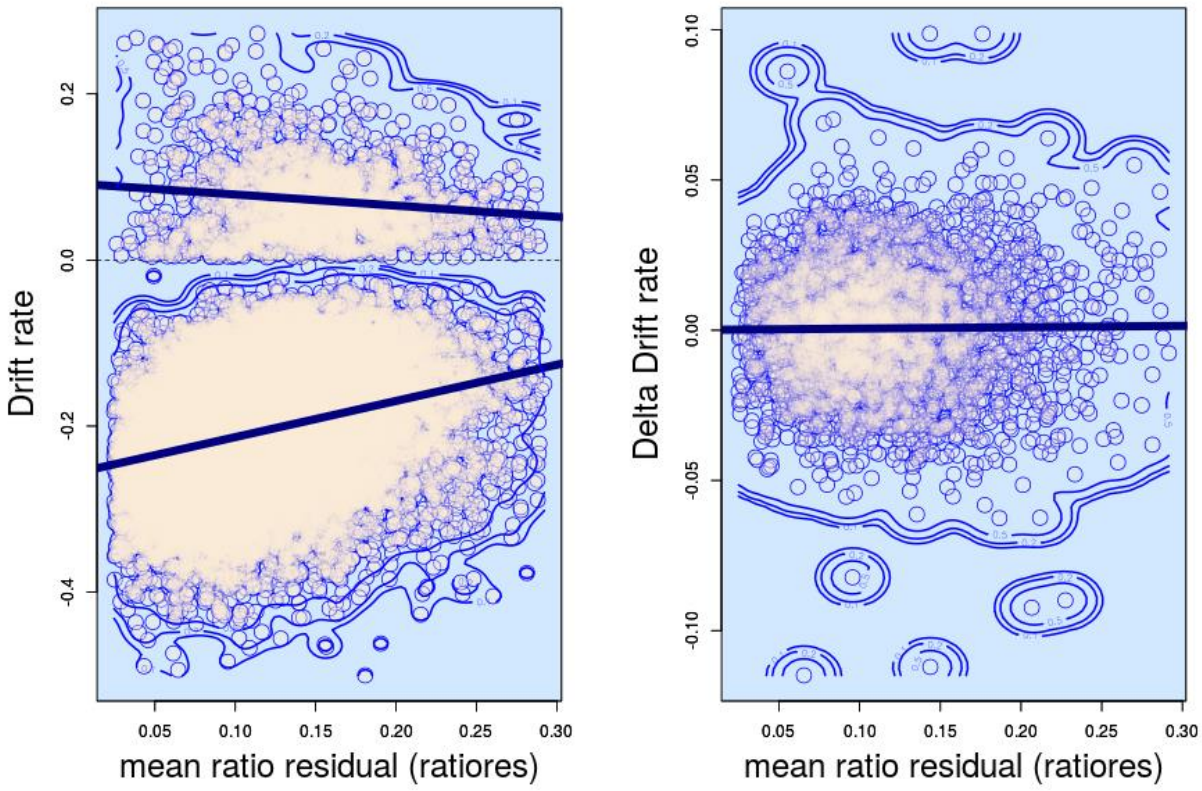


Figure 5.4. Relationships between the drit rate and the Δdrift rate and the mean residual:depth ratio (ratiores). Fitted least square regressions are included to reveal the nature of the relationships between them. Drift rate was further split in accordance with the drift rate sign to allow opposite relationships to be revealed

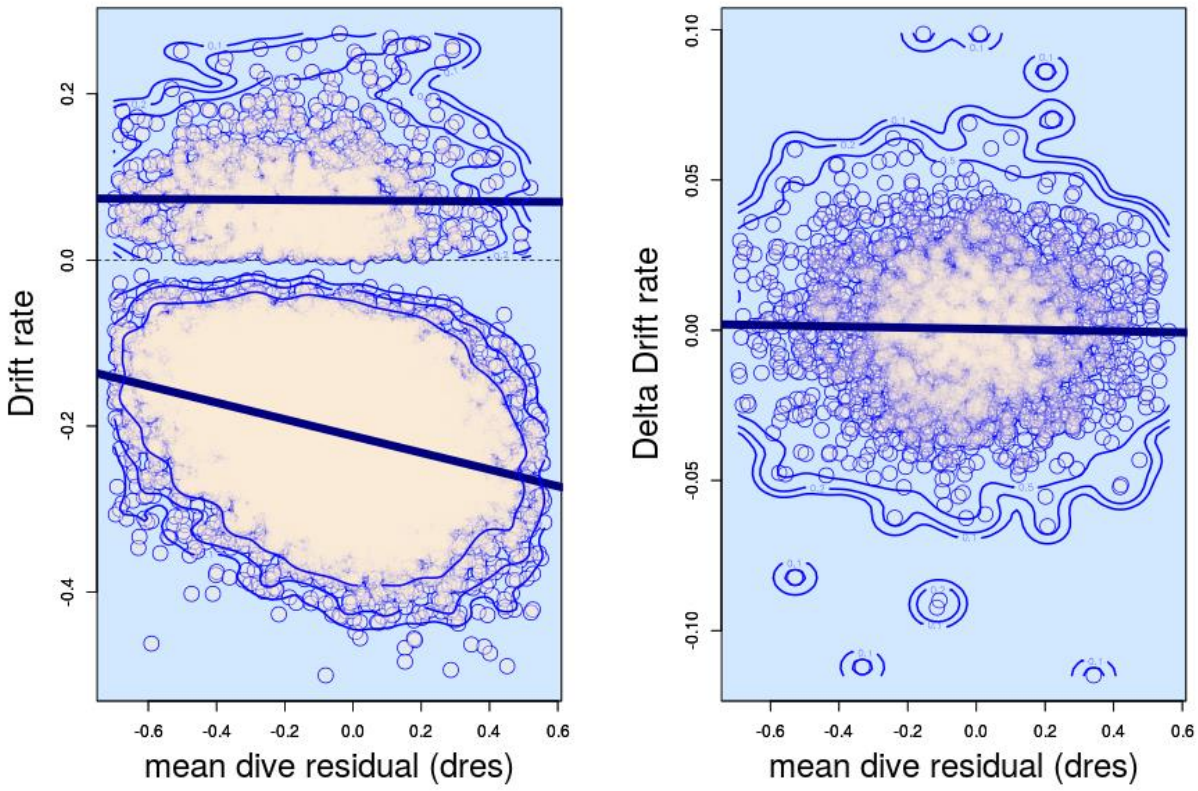


Figure 5.5. Relationships between the drit rate and the Δdrift rate and the mean dive residual. Fitted least square regressions are included to reveal the nature of the relationships between them. Drift rate was further split in accordance with the drift rate sign to allow opposite relationships to be revealed

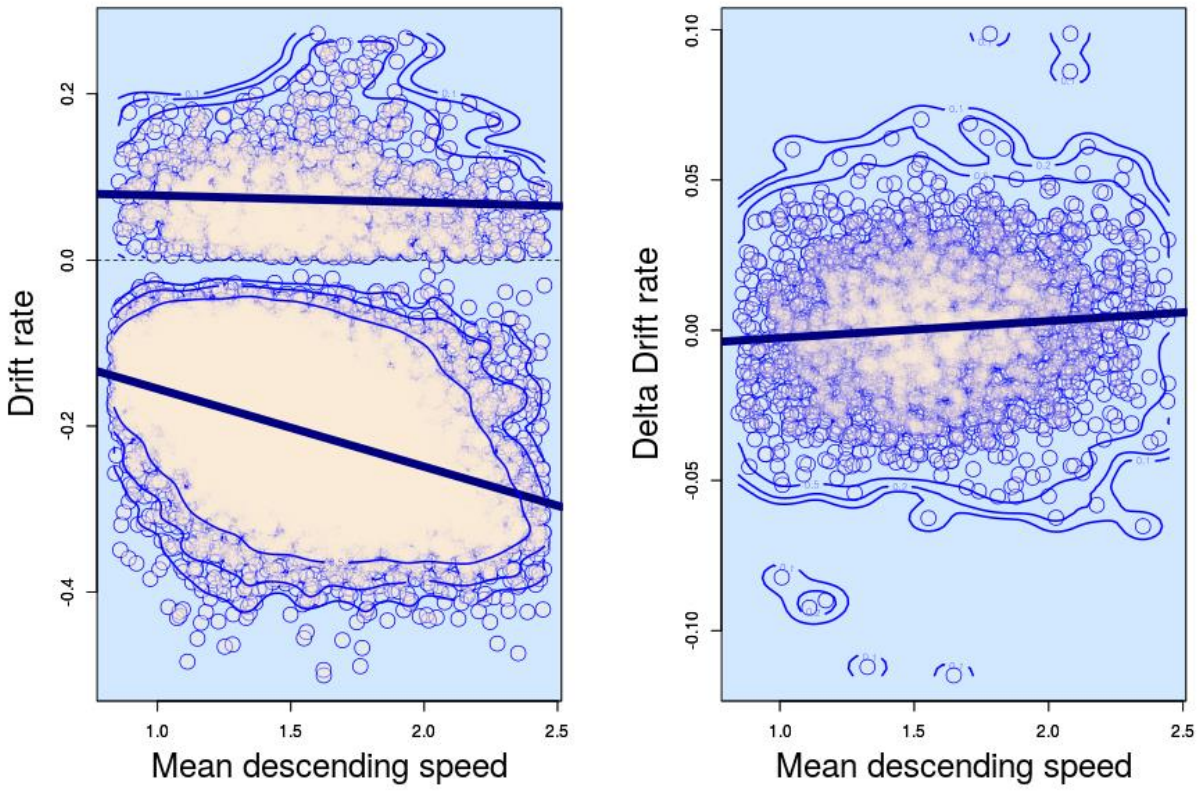


Figure 5.6. Relationships between the drit rate and the Δdrift rate and the mean descending speed. Fitted least square regressions are included to reveal the nature of the relationships between them. Drift rate was further split in accordance with the drift rate sign to allow opposite relationships to be revealed

5.7 Supplementary material

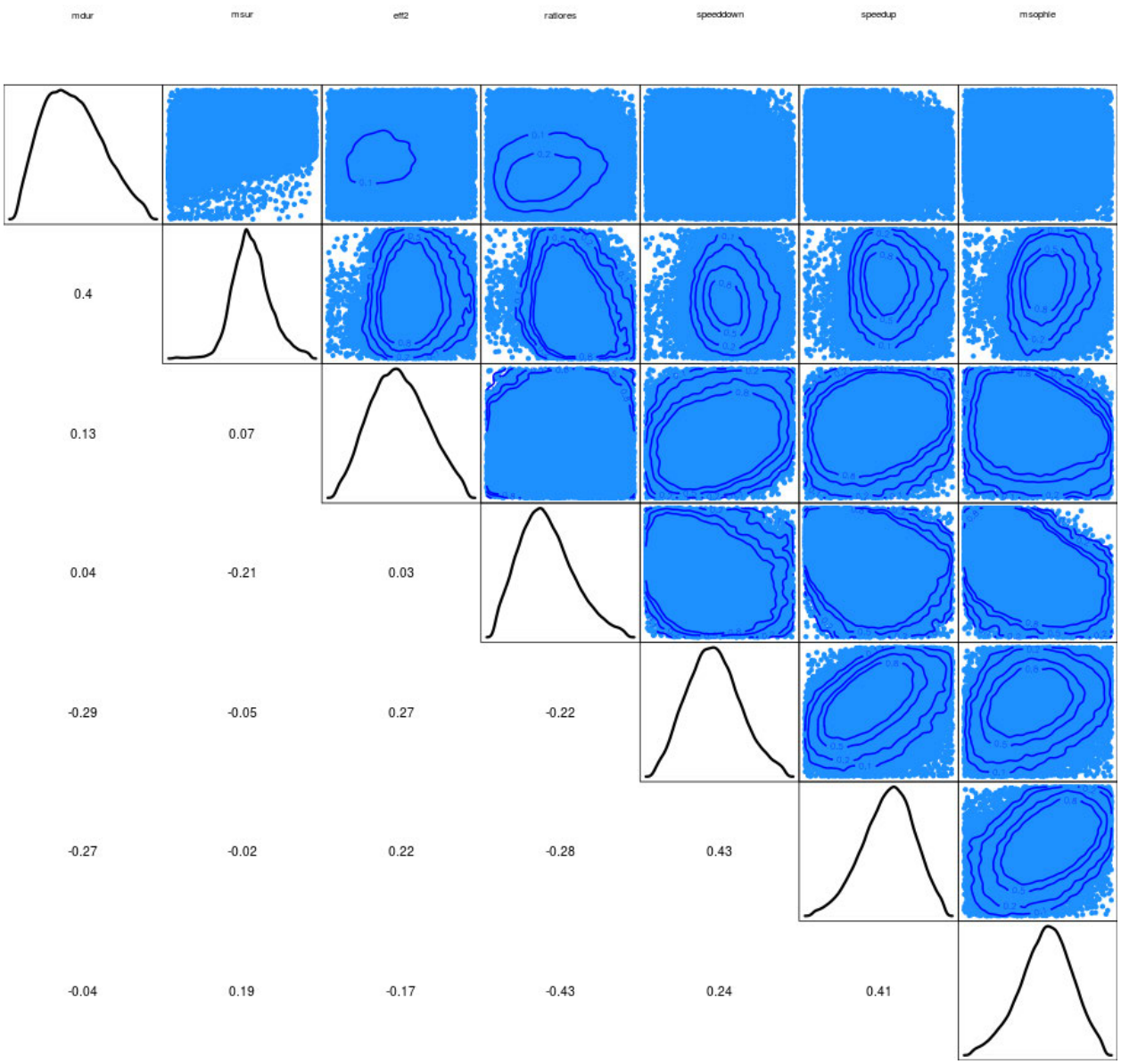


Figure S1. Correlation matrix for the suite of dive metrics considered in the drift rate and Δdrift rate models.

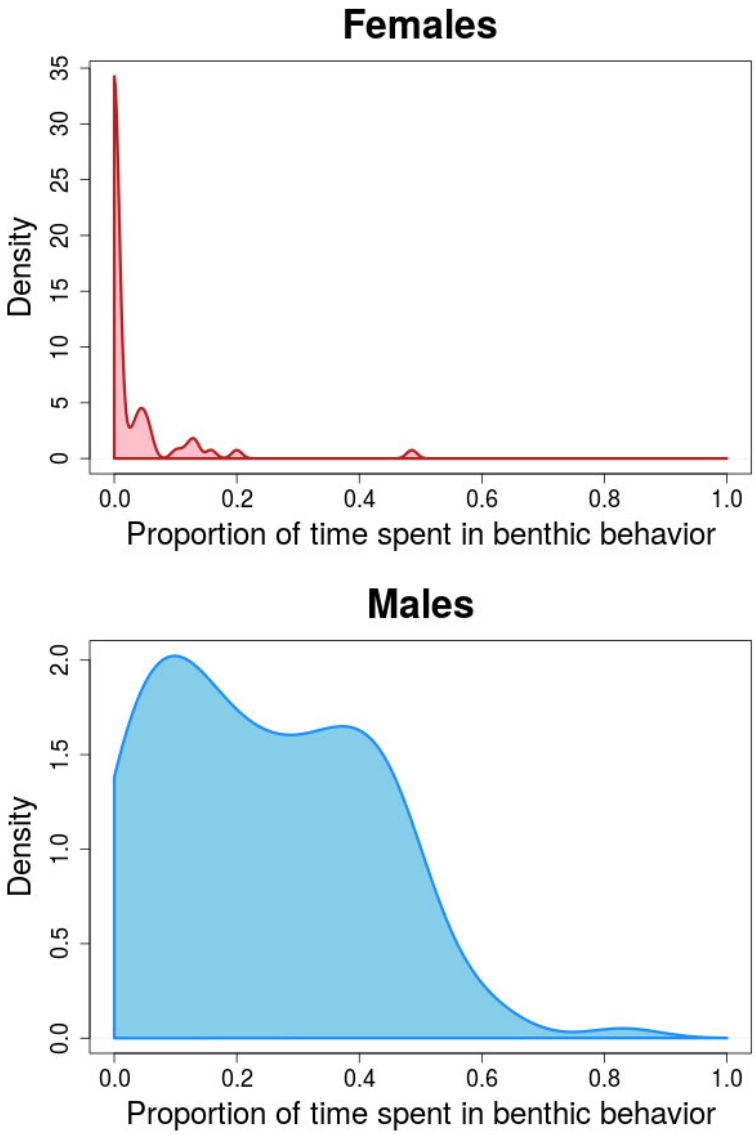


Figure S2. Proportion of time spent on benthic behaviour. Most females spend little to no time performing benthic behaviour. Most males spend a certain amount of time in benthic behaviour.

Chapter 6 Synthesis and perspectives

6.1 Introduction

The main aim of this thesis was to develop a robust approach to extract drift dives, and their associated drift rates, from compressed satellite-relayed dive information widely available for southern elephant seals (*Mirounga leonina*). Chapter 2 was devoted to this methodological advancement, and chapter 3 demonstrates how this approach has been made fully reproducible and available to the research community in the form of an open source contributed R package. Robust estimation of the drift rates across an extensive dataset allowed me to examine spatial signatures, and identify local differences in the forage habitat quality of the east Antarctic region from the perspective of a large predator (chapter 4). Specifically, it allowed me to quantitatively evaluate the importance of Antarctic coastal polynyas (during their inactive or post-polynya periods) as locations of enhanced foraging success. Finally, in chapter 5 I made inference on the body condition and changes indrift rate, in relation to seal's diving behaviour and forage strategies, within the context of expectations from ecological theory.

These analyses have provided a significant contribution to the current knowledge of the at-sea behaviour of southern elephant seals. In this final section, I integrate linkages between foraging success, movement behaviour, and the physical environment together within the context of the specific life-history tactics for males and females. Final perspectives outline future directions and improvements available for the study of at-sea behaviour using satellite-relayed information.

6.2 Maximising the utility of compressed satellite relayed dive information

Notwithstanding some limitations to the usability of the compressed dive profiles, in chapter 2 I have successfully developed a quantitative approach to classify drift dives, for periods of both positive and negative buoyancy. The method presented is much more flexible than previously developed approaches (Gordine et al. 2015), and the individual time-series of body condition matches the expectation for capital breeders and moulters. The individual seals processed in chapters 4 and 5 showed lower body condition at the start of their foraging trips, followed by a progressive increase albeit at a variable rate. During the lengthy, post-

moult trips, some individuals reached positive buoyancy and maintained this for extended periods of time; in chapter 4, the most rapid recovery of body condition was associated with an enhanced foraging success mediated by coastal polynyas. The results found from the analysis of body condition and a set of dive metrics extracted from the compressed dive profiles are congruent with the results found in the literature, based on experimental modifications of the seals body condition, or by the use of high resolution accelerometry and diving data (Adachi et al. 2014, Jouma'a et al. 2016, Orgeret et al. 2019).

6.3 Environmental variation and foraging success

The Southern Ocean shows a high degree of environmental heterogeneity. It comprises both Antarctic and sub Antarctic productive shelf regions, and vast, deep oceanic waters with characteristics determined by major circumpolar currents and frontal systems. All these marine systems are subject to inter-annual variation in environmental conditions and elephant seals are known to modify their behaviour in relation to their immediate physical environment and foraging (prey field) conditions (Bradshaw et al. 2004, Bailleul et al. 2007b, Biuw et al. 2007, McIntyre et al. 2011a). The Antarctic shelf shows particularly high seasonal variation, from a generally productive pelagic environment during the summer season to a light-limited, ice-covered environment during the winter (Arrigo and Van Dijken 2003, Arrigo et al. 2015).

The northern edge of the advancing winter sea-ice extent seems to present an optimal foraging ground for female elephant seals (Bailleul et al. 2007a). During winter, females need to accumulate energy for future breeding purposes, and one clear strategy is to forage in and around the marginal ice zone (Labrousse et al. 2015, 2017). Changes in the sea ice extent may have different impacts at different scales. For example, an increase in the winter sea-ice extent has a negative effect on Macquarie Island population (McMahon et al. 1999, 2000b, Hindell et al. 2017). As capital breeders, the energetic resources available to nurse pups are reliant upon how much energy can be accumulated during winter (post-moult) foraging trips, impacting the survival and behaviour of weaned pups (McMahon et al. 2000b, McMahon and Burton 2005, Orgeret et al. 2019). Thus, long term environmental changes leading to decreased maternal foraging success can impact population trends (McMahon et al. 2017, Hindell et al. 2017, Clausius et al. 2018), but these effects may differ across populations and species (McMahon et al. 2003, Massom and Stammerjohn 2010, Constable et al. 2014).

Immature male elephant seals, in comparison with the females, are known to forage inside the winter pack ice and also to target coastal polynyas over the east Antarctic shelf (Malpress et al. 2017, Labrousse et al. 2018). Polynyas – recurrent areas of open waters within the sea ice – are known to support earlier spring phytoplankton blooms, and are responsible for a major part of the primary production in the Antarctic region (Arrigo and Van Dijken 2003). Polynyas are known to be targeted by a large variety of air-breathing predators (Karnovsky et al. 2007, Smith et al. 2014) and are considered of importance both as predictable sources of open water for ice-obligated species, but also as key foraging locations; for example, the productivity of polynyas has been found to influence the pup production of ice-dependent seals (Paterson et al. 2015). Here, I have shown that Antarctic polynyas are also of importance to marine predators that are not ice-obligated, like southern elephant seals. Southern elephant seals, particularly males from the Kerguelen plateau population, often travel south to Antarctic waters to forage (Biuw et al. 2007; Hindell et al. 2016). My work in chapter 4 was able to quantify that of those individuals choosing to forage within the Antarctic region, individuals who target coastal polynya regions exhibit an enhanced foraging success as their body condition recovers at a faster rate than those not using polynyas. Since these are immature males, they do not yet have strong breeding 'obligations', and consequently their foraging choices may be less constrained by issues such as being trapped by ice encroachment (Bailleul et al. 2007). Indeed, males that moult on the Antarctic coast are thought to remain there year-round. It remains unclear why not all immature males choose to forage within polynyas, but not all coastal polynyas are equally productive (in terms of either ice production or biological production, see Arrigo (2003) and Arrigo et al. (2015)) and there remains a vast spatial area over the east Antarctic shelf and along the shelf break that likely also provide foraging habitat sufficient to rebuild energy reserves, albeit at a potentially slower rate (chapter 4).

6.4 Seascape of fear and risk management in the southern elephant seal

The strong spatial and behavioural segregation found between males and females is clearly not explained by individual heterogeneity alone. In nature, there is no such concept as "a free lunch", and each decision is constrained by trade-offs. The selection of a foraging location often represents a compromise between the expected reward in terms of foraging success, and the

perceived added risk in terms of jeopardising future survival, generating a so-called 'landscape of fear' (Gaynor et al. 2019). The only elephant seal predators known to be present in the Southern Ocean are southern sleeper sharks (*Somniosus antarcticus*) and killer whales (*Orcinus orca*). Killer whales are known to actively target elephant seals, of any size, at the sub-Antarctic breeding colonies (van den Hoff and Morrice 2008, Reisinger et al. 2011). At Macquarie Island, killer whales were responsible for 15 out of 20 (75%) bite wounds examined on elephant seals (van den Hoff and Morrice 2008). They are also present in the Antarctic shelf region and have been spotted within the sea ice during winter (Gill and Thiele 1997, Thiele and Gill 2007). Southern sleeper sharks are benthopelagic ambush hunters, known to include marine mammals in their diet (Cherel and Duhamel 2004) and to attack elephant seals (van den Hoff and Morrice 2008). Their known distribution also includes the sub-Antarctic shelf regions surrounding elephant seal breeding colonies, making them a potential predator of small sized seals; specifically, those that forage benthically (Cherel and Duhamel 2004, van den Hoff and Morrice 2008).. From the bite-wound study mentioned above, 18 of the 20 (90%) injured seals were in fact males, contrasting with the island's heavily skewed sex-ratio of 12:1 females to males (van den Hoff and Morrice 2008).

The results I found in chapters 4 and 5 clearly point out that males forage consistently in the benthic areas of the Kerguelen plateau, where sleeper sharks inhabits, and in the Antarctic shelf, where killer whales are common. Males also have been found to forage in the polynyas, and remain year round, during the Antarctic winter (Labrousse et al., 2018, chapter 4 of this thesis), while females make a limited used of them, even during the summer. These together suggest that females may be taking safe strategies, first, by avoiding potential predation events in the benthopelagic region, and second, by avoiding potential encroachment inside the polynyas that could prevent them to return to the colonies at the onset of the breeding season. Males, on the other seems to be adopting high risk – high reward strategies. Foraging on the benthic regions of the subantarctic plateaus exposes them to large energy-dense prey (most notably toothfish) and at the same time to the sleeper sharks. The strength of this trade-off certainly decreases with time. As elephant seals grow, they are less likely to suffer of predation from the sleeper sharks, as male elephant seals will soon outweigh sleeper sharks. Thus the risks of foraging benthic in the plateaus will soon diminish for males but would remain for females, that are much smaller than males and have limited growth once their reach sexual maturity.

6.5 Physiology in relation to mechanistic movement models

Chapters 4 and 5 together increase the knowledge of horizontal movement behaviour and foraging decisions of marine predators. In chapter 4 I present quantitative results demonstrating clear increases in relative body composition in relation to area restricted search (ARS) movements, and that these ARS movements are closely associated with coastal polynya areas (chapter 3, figure 2). ARS behaviour has been found around predictable oceanographic/physical features that can be traced by the seals (shelf regions, seamounts, polynyas).

The results I present in this thesis confirm however, that foraging activities of elephant seals are not limited only to periods of ARS, exposing the limitations of ARS analysis for detecting successful foraging regions. Elephant seals in transit heading southward to the Antarctic region start to exhibit Drift diving behaviour at variable distances (chapter 4). The decision to forage or not may depend on the amount of remnant (post-moult) body reserve. Some of the seals found transiting from the breeding colonies showed a lack of increase or even a slight reduction of their body condition (chapter 3, figure 3), suggesting that there is a trade-off between fast transiting and foraging. Foraging during these periods may not be very profitable, but a requirement for those individuals with limited reserves.

The results of foraging during transit are broadly consistent with previous analyses of movement behaviour and prey-capture in highly mobile albatrosses (Weimerskirch et al. 2007), and indicate that finding suitable prey is not necessarily enough to trigger classical ARS behaviour. In the case of the elephant seals, their continuous deep diving behaviour, even during transit, likely exposes them continuously to the deep scattering layer that comprises a large array of different potential prey types. That allows them to predate, if needed, during periods of transit without modifying their horizontal behaviour. Notably, elephant seals actively tracking mesoscale features (Bailleul et al. 2007b, 2010b, Siegelman et al. 2019) to forage could potentially generate horizontal displacements similar to transit behaviour, confounding the classification of these periods as transit or uncertain. Indeed, some of the foraging occurring during transit movement could be due to perfect coupling between the seals and filamentous prey fields along oceanographic features (Furey et al. 2018).

6.6 Perspectives: managing Southern Ocean resources

This thesis has been restricted to analyse data from elephant seals instrumented in the Indian sector of the Southern Ocean. However, the approach has been proved robust enough to clearly identify specific regions of the Antarctic shelf, the coastal polynyas, having a positive impact on the success of individuals foraging there. Given the large and growing database of satellite-tracked elephant seals, a new global integration of all elephant seal tracking data would be of major interest. This would provide a significant update to the seminal circumpolar work of Biuw and colleagues (2007). Furthermore, there has been a massive community effort to integrate multispecies telemetry data under the Scientific Committee on Antarctic Research (SCAR) Retrospective Analysis of Animal Tracking data synthesis (RAATD). This compilation evaluates the different regions of the Southern Ocean used by multiple marine predator species, to inform policy makers aiming to protect ecologically significant marine areas. This effort would be extremely benefited by integrating not only the areas in which multiple species aggregate, but also providing a metric of their relative value (forage quality) for sustaining predator populations. Some concerns regarding the negative impacts of fisheries and Antarctic seals populations have been already raised (Salas et al. 2017), but the only species that can generate robust data of this kind is the southern elephant seals. Long term time series of elephant seals foraging success, continuing into the future, can potentially provide an ecological indicator of relevance to policy makes; for example, being used to find out whether the extraction of resources from regional fisheries translates to negative effects on upper trophic levels.

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